VOL. 68

BULLETIN
OF THE
TORREY BOTANICAL CLUB

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PUBLISHED FOR THE CLUB MONTHLY
EXCEPT JULY, AUGUST AND SEPTEMBER

BY

GEORGE BANTA PUBLISHING COMPANY
MENASHA, WISCONSIN

... $4.00

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Morphogenesis in Polysphondylium

R. A. Harper

(with plates 5–9)

The problems of morphogenesis are at least becoming more clearly formulated. The new evidence of the effectiveness in plants as well as animals of form and growth determining stimuli transmitted by specific cell products (Went, 1927) puts the conceptions of cellular and tissue interactions on a much more definite basis. With the tendency to recognize the so-called mechanism of heredity as adequately elucidated, it is recognized also that the solution has so far yielded relatively little in the way of data as to the processes by which the chromosomal factors in the egg come to expression and determine the characters of the adult organism. Real progress has been made. In place of the simple factor per character, or the even simpler presence and absence conception, it is now sometimes assumed that all the factors may influence all the characters. This is an advance toward a recognition not only of the real complexity of the problem but also of the facts of correlation, of the interrelation of the parts, in the make-up of the organism as a whole, as contrasted with the conception of organic unity as being nothing more than the chance aggregation of hard and fast unit factors—the *Anlage* of specific unit characters.

The general facts of the life history and method of building the sorocarps of *Polysphondylium* are well known from the studies of Brefeld (1869), Van Tieghem (1880), Olive (1902), and others. I have endeavored by a more detailed study of the activities of the myxamoebae and the pseudoplasmodium to discover the morphogenetic factors involved in their behavior and the building of the mature plant with its differentiation of soma and spore plasm. I have, as with *Dictyostelium* (1926), endeavored to bring out the essential facts in a series of photographs. The quality of these photographs leaves much to be desired. The excuse for this is, again, the inherent difficulty of the material. All the figures of mature plants were made from petri dish dung agar cultures photographed from above, the

[The Bulletin for April (56: 181–226) was issued 13 June 1929.]

plants having curved over sufficiently to permit getting the low magnification views as shown.

In its structural specialization *Polysphondylium* goes a step farther than *Dictyostelium*. Its sorocarps show secondary lateral elements or branches, as well as the central axial stipe and terminal sorus characteristic of *Dictyostelium*. As in the cormophytes these branches are essentially replicas of the central axis on a smaller scale and with changed tropistic response. The development here, as has been shown for the Boston fern, is one of reduplication of parts (Benedict, 1916), or homoeosis (Bateson, 1894). Another step would naturally be the development of tertiary and further successively subordinated series of branchlets. Such types are known in the Thamnidieae and various other groups of fungi and in *Caulerpa* and many other algal forms. Uittien (1929) has recently pointed out that there is correlation in very many cases between the type of venation in the leaf and the type of branching of the inflorescence, a phenomenon which suggests that the physical background underlying such phenomena as homoeosis may also be common to both determinate and indeterminate growth forms.

As in my study of *Dictyostelium*, I shall call the completed plant the sorocarp; its main axis, the stipe or sorophore; the terminal and lateral spore masses, sori. For convenience, without implying morphological equivalence, we may call the points of origin of the whorls of branches nodes, and the segments of stipe between the nodes the internodes; node and internode constitute a phyton (Gaudichaud, 1841). The portion of the stipe between the uppermost whorl of branches and the terminal sorus we may call the terminal segment. The pseudoplasmodial mass after it has left the substratum and is building the stipe and branches we may call the sorogen or sorogenic mass. The form changes by which the myxamoebae fit themselves together in building the stipe with its evenly tapering outlines, dense parenchyma-like structure, and curves developed to maintain its balance, we shall regard as before as involving morphallactic transformations in cell form. The creeping, definitely oriented translocatory movements, by which the myxamoebae move upward to build the stipe and outward to build the branches we may call respectively anallactic and diallactic amoeboid movements.

I shall, for convenience, consider these pseudoplasmodial types in which the mature plant shows a clear differentiation of soma and germ plasm as semi-coenobes. I have elsewhere (1926) discussed the evidence that such forms illustrate at least transition stages between protophytes and metaphytes. For convenience, also, I shall distinguish the processes of cell enlargement by food assimilation and cell multiplication by division as respectively mass growth and census growth. That both morphogenetic and intracellular cell differentiation resulting in organogenesis and histogenesis are phenomena that can advantageously be considered in a special category of life processes, distinct from growth in size, is well shown in the life history and development of *Polysphondylium*.

Structure of the mature plants. Before describing the growth and morphogenetic processes by which the plants are formed, we may note the general facts as to their appearance, symmetry, size-relations, etc. The range of variation in size, number of branches, and general proportions of the plants of *Polysphondylium* is comparable to that in the higher fungi and algae and in the seed plants. This is shown in the figures of plate 5, which are chosen to give an idea of the apparently fluctuating variability of the sorocarps as they develop on dung agar in petri dish cultures. I have so far not attempted to isolate races by selection and propagation of the various types which appear in such populations. The species with which I have worked is apparently *P. violaceum* Bref. My material was obtained from cultures of rabbit dung on garden soil as described by Krzemieniewscy (1927).

As is well known, *Polysphondylium* may produce simple unbranched sorocarps and occasionally *Dictyostelium* is branched. However, the branched colonies of *Dictyostelium* which I have seen are of the type shown in my figures 5 and 6, plate 6 (1926), in which it is possible that the branch was not developed as a segment from an apical sorogenic mass but was formed by a second colony of myxamoebae which crept up the stipe of an already completed sorocarp to a point favorable for the formation of its own plant body and then developed what appears to be a branch. Olive (1902, p. 480) speaks of branches of *Dictyostelium* formed in both ways. Unbranched forms of *Polysphondylium*

(pl. 5, figs. 1, 2) are much more common in my experience than are branched forms of *Dictyostelium*. These unbranched forms may occur in the same petri dish culture mingled with others which have reached the full normal development with eight or ten whorls of branches. They in general are to be regarded as diminutive or slender forms, though well proportioned as to tapering of stipe and size of sorus. The relative number of cells in the stipe is obviously larger than in the case of the plants with many branches. Figure 3 shows a sorocarp with only a single lateral branch which was apparently formed from a segment of the terminal mass though its development was not seen. Its size both as to length of stipe and diameter of sorus suggests that it represents perhaps the simplest possible expression of the tendency to form whorls of branches on the main axis. The diameter of the lateral sorus as compared with the terminal sorus is a little large, about 1 :1.6, instead of the general average of about 1 :2. The entire height of this sorocarp is not shown, as the base of the stipe was hidden by the substratum. I have occasionally seen sorocarps with a single lateral sorus having a very short stipe or no stipe. Such a case is shown in figure 4. In figure 1, there is also a small lump about half way up the stipe which may be a mass of slime or may contain amoebae.

Figure 5 shows a sorocarp with a single whorl of three branches, and perhaps more normal proportions, though here again the full length of the stipe is not shown. The average diameter of the lateral sori compared with that of the terminal sorus is about 1 to 2. The relative length of the terminal segment of the stipe to that of the branches is of the same general order here as in the more branched sorocarps shown in figures 8, 9, and 14, 15, 16.

The branched sorocarp in figure 6 shows a form with the terminal segment unusually short, giving the plant a stunted appearance as compared with the more common forms. Such types are quite unusual. Figure 6 shows also a simple unbranched sorocarp (6b) arising from nearly the same region of the substratum from which the branched sorocarp (6a) arises. This close association of sorocarps is not uncommon in my cultures, and frequently at least the unbranched sorocarp is formed later. Figure 7 shows

a plant with two nodes, the upper one with a single branch, the lower one with three branches. Figure 8 shows another plant with two whorls, the lower with three and the upper with two branches. The internode is relatively short and the terminal segment much longer than the internode, and the latter is also relatively much longer than the terminal segments in plants 7 and 10. Figure 9 shows a plant with two whorls of four branches each, the relative lengths of the internode and the terminal segment being more nearly normal. Figure 10 shows a rather normally proportioned plant with two whorls of branches, four branches at the lower node and three at the upper.

The plant shown in figure 11 has a fairly symmetrical development, with the number of branches in the whorls counting from below 3, 3, 4, 4, 1. The apical and basal whorls show fewer branches than those in the midregion. On the other hand, figure 13 shows a plant with an irregular distribution of branches, the numbers being, counting from below, 3, 1, 2, 4, 4, 4, 4, 3. Figure 12 shows a plant with unusually numerous branches in the lower whorls. The series of whorls of branches shows 2, 1, 6, 6, 5, 5, 5, 4. The average number of branches per whorl for this plant is 4.25, against 3.1+ for all the plants shown on plate 5. The whorl of branches at the third node from the base is strangely one-sided instead of radial, five branches extending more or less to the right of the stipe and only one to the left. Variation in the length of the branches and the size of the sori they bear is conspicuous. The fourth and fifth nodes from the base each have one branch very much shorter than any of the others, and they bear correspondingly diminutive sori.

The plant shown in figure 14 is quite symmetrical in its form. It has two branches in the basal whorl and one in the apical whorl, with five median whorls of three branches each. Figure 15 has an unusual combination, with its lower three whorls showing two branches each and its upper four whorls with three branches each. Figure 16 shows the plant with the largest number of whorls in a single series which we have yet photographed. It has eleven whorls of branches, with the number of branches per whorl from the base up 4, 4, 3, 4, 3, 3, 2, 2, 4, 3, 3.

The range and general character of the variations in such a series of semicoenobic plants as noted above is in general quite

comparable to the diversity in form and general proportions in higher plant types and in view of the nature of the morphogenetic processes by which these forms are produced this similarity in end results is notable. We have small plants of relatively normal (fig. 10) and stunted (fig. 6a) habit. We have average sized plants with a tendency to regularity in form and the numerical distribution of their parts (fig. 11) and others with notable irregularities in these particulars (figs. 13 and 16). The difficulties in getting the plants properly placed for photographing make it difficult to bring out adequately these facts as to their general habit.

TABLE 1

Relative dimensions of the parts as shown in a series of twenty-eight plants

Ratio of average height to first whorl of branches to average total height	1 : 2
Ratio of average length of terminal segments to average total height	1 : 3.8
Ratio of average length of internodes to average total height	1 : 5.3
Ratio of average diameter of terminal sori to average length of terminal segments	1 : 4.5
Ratio of average diameter of lateral sori to average length of branches	1 : 2.5
Ratio of average diameter of lateral sori to average diameter of terminal sori	1 : 1.9
Ratio of average diameter of terminal sori to average total height of branched plants	1 :17.1
Plants with no branches	
Ratio of average diameter of terminal sori to average height of plants	1 :10
Ratio of average height of unbranched plants to that of branched plants	1 : 2.6
Ratio of average diameter of terminal sori of unbranched plants to that of branched plants	1 : 1.6

The percentage distribution of cells to soma and germ tract tends, more or less, to be preserved whether the colony is large or small. This is all the more remarkable since the determination is apparently achieved at the time when the base of the stipe is being formed. It seems likely, however, that in the long run the relative number of amoebae massed together at the time the

stipe base is started is a fair index of the number that will probably be present in the later stages of differentiation of the sorocarp.

The most constant dimensional elements are the distances between the whorls of branches, the relative length of the branches in successive whorls, the distance between the last whorl of branches and the terminal sorus, and the relative diameters of the lateral and terminal sori. The terminal sorus is always larger than any one of those on the lateral branches. The sori on the branches of a whorl vary in size with the length of the branch which bears them. Certain of these dimensional relations as measured with the horizontal microscope on 28 sorocarps grown in small test tubes are given in table 1.

There is perhaps a tendency to form fewer branches in the basal and apical whorls, though this by no means always comes to expression. Six plants shown in plate 5 (fig. 7, 8, 11, 12, 13, 14) have fewer branches on the terminal node than on the one next below. In sixteen plants from a single culture, whose number of whorls varied from three to eleven, the average number of branches on the basal node was 2.5+, on the distal node was 2.8+, while the average for the remaining nodes was 3.6. The larger sorocarps may have as many as fifteen whorls of branches.

Free swarming and aggregation stages. The myxamoebae may be quite different in appearance at successive stages in their development. Figure 17 shows them moving rather sluggishly in a hanging drop dung agar culture, and tending to remain about isodiametric in their general outlines. In figure 18 they appear more slender and elongated and are creeping about somewhat more actively, though not showing any evidence of a concerted movement in a specific direction.

I have worked for the most part with richly nourished cultures of *Polysphondylium,* in which the amoebae become very numerous within the first twenty-four hours. In such cultures when they come to maturity the myxamoebae very soon form thick dense strands converging on the site of the future sorocarp. In such streaming strands the movements of the individual myxamoebae cannot be followed. Rivers of myxamoebae extend frequently for long distances across the culture medium. In petri dish dung agar cultures of *Polysphondylium* I have ob-

served no tendency to the choice of any specific type of loci for the formation of the sorocarps. In my hanging drop cultures of *Dictyostelium* the sorocarps were quite commonly formed at the edge of the culture liquid. When the surface of the medium is scratched and a furrow made by the inoculating needle many of the first formed sorocarps of *Polysphondylium* are in or near this roughened region. This makes difficult the microscopic study and photographing of the base of the stipe in such cases. In well-developed cultures, however, the sorocarps are rather evenly distributed throughout the area of the petri dish. There is no evidence of the formation of concentric zones of sorocarps. Their development from day to day is in quite irregular and patchy groups.

In the case of *Dictyostelium* my cultures were made and figures of the aggregation stages chosen to illustrate the behavior of the free amoebae as they collect to form the sorocarpic mass (1926, plate 7, figs. 17-22). Such stages were relatively neglected by the earlier workers. For *Polysphondylium* I have photographed the more massive pseudoplasmodia as they flow together to start sorocarp formation. My observations confirm in general the data given by Brefeld (1884) and Olive (1902). Stages in the process of aggregation to form sorocarps are shown in figures 19, 20, and 21.

Figure 19 shows the central portion of a rather symmetrical radially well-developed pseudoplasmodium in which the young sorocarp is merely a central mass toward which the radiating streams of myxamoebae are creeping. There are about ten main elements in this converging system. Each of these is made up by confluence of smaller streams. The larger of these strands meet as a rule at angles of less than 45°. There are, however, especially toward the center, many smaller laterals which may enter the main streams at angles of 60° to 80°. Anastomoses between the smaller branches are not uncommon.

Figure 20 shows the central mass developed further into an upwardly extending conical or cylindrical column. The end of the cylinder is enough out of vertical so as to appear in the photograph, taken from above, as a dark, short, finger-like stub projecting upward in the figure. About ten main converging streams are shown in this figure. The confluence of smaller

streams to make these larger pseudoplasmodial elements is shown as in figure 19. The fringe-like, smaller streams coming into the large streams at wider angles are not so much in evidence. The main streams hence appear more clean-cut. As only the central region of the system is included in the figure, the peripheral shortening of these main streams as a result of the centripetal flowage is not shown. Figure 21 shows the same pseudoplasmodium which is shown in figure 20, more highly magnified and a few minutes later. Various minor differences in the smaller branches can be made out, though the general configuration is unchanged.

Figure 22[1] shows a young sorocarp further advanced in its development, but with the outlines of the pseudoplasmodium which formed it still plainly shown on the substratum. The young sorocarp forms a somewhat S-shaped curve, and is sufficiently out of the vertical to make possible the photograph as shown, looking down on the culture from above.

The whole system of pseudoplasmodial branches in this case, as happens many times, was quite one-sided. The streams of myxamoebae formed a watershed-like system of many stream lines, thinning out and branching repeatedly toward their extremities. As noted, the streams of myxamoebae leave paths or furrows in the agar medium which persist after all the amoebae have reached the central mass. At the magnification used in these particular figures it is not always easy to be sure in the photograph whether a given converging element in such a system is made up of the streaming amoebae themselves or is merely the track they left in the agar. In either case the orientation of the converging streams is correctly indicated. In the present case (fig. 22) the pseudoplasmodial outlines, for the most part, at least, merely mark the paths made by the streams in the agar; while the pseudoplasmodial mass itself has now become largely, if not wholly, the young slightly S-shaped sorocarp. The nature

[1] This particular figure is confused by the presence of the lower portion of the stipe of another completed sorocarp which has its base a little above and to the right of the one which is being formed. This segment of stipe appears as the thick, black line curving in a wavy direction downward to the base of the figure and gradually going out of focus. It has no relation to the sorocarp under consideration.

of the morphogenetic process as one of cell translocation and not of growth is thus sharply visualized. The branching slimy furrows which the streaming mass left behind persist for some time in the substratum. The pseudoplasmodial mass of cells has transformed itself by specifically oriented synallactic creeping movements into the more or less erect columnar young sorocarp. From the standpoint of the stimuli involved there is here exhibited a sort of centrotropy whose expression may be compared to the *Suchbewegungen* of the elements of the higher plants, as Janse has recently distinguished them (1927). The obvious distinction to be recognized is that the movements of tendrils, twining stems, growing points, etc., involve no extensive changes in the spatial interrelations of the cells of which the moving parts are composed. The advance of a root tip is due to the specifically oriented enlargement of the daughter cells and their division, when mature, in specially determined planes. It is a matter of growth movement; but the distinction between such oriented growth movements and creeping movements is largely one of degree. The wanderings of the free amoebae on the substratum in their growing stages (figs. 17 and 18) necessitate extensive creeping, specifically oriented translocations, in order to bring them into the mutually compacted relations which the root cells never lose. That in both cases the movement is the expression of the oriented activities of the individual cells as such is obvious in the light of the phenomena in *Polysphondylium*. The stimuli which determine this centripetal migration, while difficult to determine specifically, are clearly not from the physical environment in even the degree suggested for *Dictyostelium*, in which the locus for a sorocarp and the direction of flowage are frequently at least, as noted, toward the drier margins of the culture medium. The stimuli are obviously attractions for each other existing between the amoebae and are in some degree at least proportional to the mass of amoebae in any given direction from the moving stream. The reactions to the stimuli are in their expression centrotropic.

That the individual amoebae are able to trail each other by chemical stimuli or physical stimuli from slime, etc., even when not in contact, is clearly suggested in my photographs of the aggregation phases in *Dictyostelium*. There is probably no reason

for assuming the existence of any other factors of stimulation in the case of the pseudoplasmodial flowage shown in figures 19-22. Much less is there any reason for assuming any superchemical or physical stimuli or the action of organizing or regulating principles associated with the multicellular organismal conditions resulting from the aggregation of the myxamoebae. The behavior of the pseudoplasmodium as a whole is the sum of the behaviors and reactions of the individual myxamoebae.

Stipe and branch formation. In my cultures the pseudoplasmodium commonly frees itself from the substratum rather early and proceeds upward as a cylindrical mass, building the sorophore to quite a height before branch formation begins. In other cases, as seems more common in *Dictyostelium*, this terminal mass remains connected for some time by a long strand or river of amoebae flowing up the newly formed stipe and extending below into the similar streams of amoebae creeping toward the base of the forming sorocarp. In typical cases before branch formation begins the whole mass of myxamoebae is aggregated in a terminal cylinder, the sorogen, at the apex of the forming stipe.

The stages at which the sorogenic mass is just freeing itself from the substratum are naturally very difficult to photograph in petri dish cultures, since the young plants rarely bend over sufficiently to give a side view from above the culture. Figure 23 shows a stage in which the stipe has reached a length about twice that of the apical sorogen which is building it. In this case there is no stream of amoebae at this stage connecting the sorogen with the substratum.

The sorogen is cylindrical, narrowed toward its base, and almost papillate at its apex, as is well shown for a later stage in figures 25 and 26. This is typical for *Polysphondylium*, and the further development of the sorocarp consists in the elongation of the stipe and the metamorphosis of the apical mass into the whorls of branches and the apical sorus. The length of the stipe, before branching begins, varies greatly and is probably more or less influenced by environmental conditions. It is difficult to get exact measurements of its length in petri dish cultures, but as noted above, measurements of 28 plants with the horizontal microscope indicate that the height of the stipe to the first whorl of branches is about one half of the total height.

The process of building the branches consists in the beginning in abstricting a thick, ring-like, cluster of myxamoebae from the base of the sorogen. Figure 24 shows such a mass already left some distance behind by the further advance of the sorogen. Such ring-shaped clusters I shall call, for convenience, segmental masses. They are successively produced in metameric order until all the whorls of branches are provided for. As many as six such masses may be cut off before the first has completed its differentiation into a whorl of branches (fig. 34).

The first indication of the cutting off of a segmental mass is the appearance of a rather broad constriction toward the base of the sorogen. This is well shown in figure 26, which represents a young sorocarp with three segments cut off and left behind in serial order and the fourth just forming. The abstriction of such a segmental mass suggests cleavage of the cellular aggregate into two unequal parts—the larger part continuing to build the stipe upward, while the smaller remains behind to form the whorl of branches. The broad constriction formed does not, however, suggest the sharp cleavage furrows found in the cutting up of the aethalium of a slime mold or the sporangia of the Mucorineae into spores. It seems more probable that what is taking place here is a sort of catenoidal break-up of the viscous colloidal sorogen, due to the successive lagging behind of masses of myxamoebae at its basal end. The myxamoebae at the apex of the stipe continue to build it higher. Those at the basal end successively reach a stage at which they cease to advance and the two groups separate as a result of the pull from above, with the more rigid stipe affording a support to which the passive basal mass is left adhering. Such serially disposed segments as are shown in figures 25, 33, and 34, suggest the catenoidal series of droplets into which a somewhat viscous thread will break up when submitted to longitudinal strain. The obvious difference here is that the stipe remains as a string on which the catenoidal beads are strung. Two successive stages in the process of constriction are shown in figures 25 and 26. In figure 25 the narrowing is barely visible but a little later, as shown in figure 26, the broad shallow furrow is well marked. The proximal slope of the furrow tends to be ridged, indicating that the myxamoebae of the segmental ring are already beginning to draw to-

gether and form a more rounded mass. The segmental mass when first cut off is typically spindle- (fig. 24) or top-shaped (figs. 25 and 26, the upper segment), but the amoebae immediately tend to draw together, reducing its surface of contact with the stipe. Very soon projections appear on the surface of the segmental masses, indicating the beginning of branch formation, and if successively older segments are compared the stages in the process may be followed on the same sorocarp (figs. 32 and 34).

It happens very frequently, as a result of the changes and disturbance incident to photographing, that the young sorocarps lop over so far that the sorogen comes in contact with the substratum. This situation leads at once to a very specific autoregulative reaction. The myxamoebae of the sorogenic mass at the point of contact with the substratum turn about and begin to once more build the stipe more or less vertically upward from the new point of support as they did from the initial point at the beginning of sorocarp formation. If the disturbing condition is recurrent this process may be repeated, resulting in a sort of successive looping down of the stipe resembling the stoloniferous growth of the common breadmold, *Rhizopus stolonifer*.

This characteristic morphogenetic reaction does not, however, prevent the normal process of sorus-formation. If branching has not begun it is delayed until anallactic migration in the new direction has carried the sorogen to the necessary distance from the substratum, when it begins to form the segmental masses and continues development until the sorocarp is complete or the process is interrupted by a repetition of the toppling over and contact with the substratum. If branching is already under way when the whole plant bends over a most characteristic situation develops, illustrating with the greatest clearness how an aggregate of free individual cells on the emergence of a new situation can alter their behavior to meet the new conditions with all the definiteness of the most highly integrated systems of tissues and organs. The new set of, in this case, spatial interrelations induces the substitution of a new specifically different set of reactions in the system; and this happens in a system of elements the cell units of which are entirely equivalent and totipotent both in their visible appearance and their reaction potentialities. Such possibilities in behavior we have been inclined to assume imply a

high degree of visible integration, and constitute one of the main supports of organismal hypotheses and the assumption of integrating principles. The series of stages in the development of a single sorocarp, which are shown in figures 27 to 31, illustrate such a situation. The pictures were taken at intervals of from ten to twenty minutes. In the stage shown in figure 27 three segmental masses have been formed. The sorogen, which has been developing soma (stipe) at its apex and abstricting segmental masses at its base in a definite rhythm, now intermits completely the latter process while continuing the former. The cellular morphallactic form adjustments, by which the smoothly tapering stipe was being formed and at the same time its balance maintained and its elongation directed away from the substratum, suddenly swing the axis of elongation of the stipe through an angle of upwards of 90° and thus tend to regain the orientation vertical to the substratum. It is to be noted that this is accomplished equally well in either erect or inverted (hanging drop) cultures. The bend in the stipe is smoothly rounded, showing the utmost nicety of adjustment between the molding cellular interactions by which the tapering form of the stipe is maintained and the cellular response to changed environment by which the new direction of elongation is achieved. The whole procedure simulates in all superficial features a growth curvature and yet there is no growth in number of cells or mass of assimilated materials. The whole process is one of coördinated creeping, anallactic movements, anaphytosis (Schultz-Schultzenstein, 1861), of individual cells and morphallactic changes in their form as they fit themselves together to build the stipe. All three segments are still in the early stages of development as merely thick, massive, ring-shaped groups of myxamoebae encircling the stipe. Meanwhile, the whole plant has lopped over. The sorogen has come in contact with the substratum and has at once begun to bend up in a new direction of anallactic migration by the amoebae. In figure 28 the new axis of advance is well fixed and the sorogen is smoothing out into its normal form. The region of contact of the sorogen with the substratum is conspicuously marked by an oblong depression in the agar medium filled with slime and with a rounded thickened mass at the end from which the stipe extends upward. In figure 29 the sorogen is still nearer the ver-

tical and has raised itself from the new point of departure by a stipe which is about one-fourth its own length. In figure 30 the new segment of stipe is about the length of the sorogen, and in figure 31, fifteen minutes later, it is a little longer than the sorogen.

In this series of stages the myxamoebae of the sorogen have thus carried out a characteristic and highly adaptive tropistic response by which, after having toppled over and come in contact with the substratum, they have attained a new foothold, turned upward and in large part regained their normal direction of migration under the influence of geotropic and hygrotropic stimuli. If we turn now to the behavior of the myxamoebae in the three earlier formed segmental masses, we find an equally specific situation. While the amoebae of the sorogen have changed their behavior under the changed conditions, the amoebae of the segmental masses proceed with their morphogenetic processes quite uninfluenced by the new space relations of the system taken as a whole. They have proceeded with the same radially oriented movements as if there had been no change in the orientation of the stipe on which they are borne; that is, they have formed branches radiating from their position on the stipe as a center. The orientation of their migratory movement with reference to the stipe is unchanged, though it is now widely different in respect to the substratum and other environmental surroundings than it would have been if the plant had not bent over. The sorogen has shown itself specifically plastic in the determination of its reaction in accordance with its position in its external environment. The segmental masses made of amoebae, differing from those in the sorogen only by position in the system, show themselves specifically fixed in their morphogenetic reactions regardless of changes in position with relation to the external environment. Such reaction complexes are of course common enough in other plants and have their interest here from the fact of their being so conspicuously matters of cell behavior even though the cells are aggregated in specifically organized colonies.

The process of leaving behind such segmental masses is rhythmically repeated until the mass of the sorogen is reduced to about the volume necessary to make a single segmental mass. When this stage is reached the stipe is built on further to some-

thing more than one and one-third times the length of an ordinary internode (table 1) and the remaining group of myxamoebae rounds up to form the terminal sorus. The lengths of the successive internodes tend to be about equal for sorocarps under constant conditions but wide divergences from type are found in petri dish cultures which are subjected to the disturbances of study and photographing.

The formation of a whorl of branches involves first the localization in the segmental mass of centers for lateral stipe formation. These are more or less symmetrically placed about the stipe, and as noted above vary in number from one to five or even six. The segmental mass is too dense to permit direct observation of the first aggregation of myxamoebae to form the basal groups of these stipe laterals. The important fact morphogenetically is that the amoebae have in erect cultures changed their tropistic reactions so that they creep out radially from the stipe. With relation to their earlier orientation they have become plagiotropic. The sorogenic mass from which they have separated continues negatively hygro- and geotropic and builds the vertical stipe still higher. The segmental mass at first draws together but almost at once begins to build radially placed lateral stipes. The process in its response relations is the same as in the case of any radial and metameric system of branches in the higher plants.

The branches appear first as projections of the segmental mass. If three branches are to be formed it becomes triangular in outline; if the whorl is to consist of four branches the segmental mass becomes four-cornered as viewed from above. The number of branches to be formed is at once indicated by the plastic change in form of the mass of myxamoebae as shown in figures 28, 32 and 34. The side view is not favorable for bringing out these forms in photographs but illustrations of two, three, and four lobed forms can be recognized without difficulty in the figures. That these form changes in the segmental masses are really determined by the formation of the lateral stipes in their interior is obvious from the shapes assumed. Each young branch rudiment is a blunt but tapering papilla rather than an oval swelling. The extension of the slender solid stipe within the plastic mass determines the shape of the projection of which it is the support-

ing axis. The stipe is built on in advance of the movement of the great mass of the myxamoebae. Its elongation is determined by the morphallactic form adjustments achieved by the myxamoebae at its apex. A little later the segmental, ring-like mass of myxamoebae in the upper whorl of the sorocarp shown in figure 29 is seen to have been thus transformed into three oblong cylindrical finger-like projections diverging from the stipe as a center.

Very soon, as in the lower two whorls in figure 29 and in all three whorls in figure 30, the lateral stipes become exposed in their proximal portions and the myxamoebae form lateral sorogenic masses which rapidly push their diallactic migrations to completion and form rounded sori. The segmental masses shown at the three nodes in figure 28 are destined to produce respectively two, one, and three branches, and this is already indicated in their form as shown in the figure. As the lateral sorogenic masses push away from the central stipe, considerable masses of slime are left as anchorage for the branches on the central stipe. The outlines of these slime masses are surface tension curves determined by the viscosity of the slime and its adhesion to the central stipe and the bases of the lateral stipes, as shown in figure 6, plate 6, in my former paper (1926).

The process by which any one branch of a whorl forms itself from a portion of the segmental mass is the same in principle as that by which the central stipe or axis is formed from the pseudoplasmodium. The branch is a lateral element attached by slime to the main axis just as the main axis is attached to the substratum by slime. As Brefeld's and Olive's figures show, there is no tissue connection between branch and stipe such as is found in the branching of algae and fungi generally. In this respect the conditions suggest an analogy with the false branching in the blue-green algae, especially those in which the base of the branch is a heterocyst and hence in some cases somewhat enlarged and rounded.

I have described in some detail and given measurements showing the rate of tapering of the stipes in *Dictyostelium*. The facts there brought out hold essentially for *Polysphondylium*, with one exception. I have noted that in *Dictyostelium* we can distinguish three regions of the stipe as to their rate of tapering:

first, the basal region in which the diameter diminishes very rapidly; second, the median trunk region in which the tapering is very slight, one unit in diameter to 112 units in length; third, the terminal region in which the tapering is again more rapid, 1 to 67. In *Polysphondylium* the median region with a quite inconspicuous rate of tapering is relatively much longer. In the apical region the tapering is again more rapid. The base of a stipe, which in this case is quite irregular and is curved to one side, is shown in figure 35. The normal form is knob-like, or bulbous. The slime mass which anchors it to the substratum is well shown. Figure 36 shows a segment of the stipe of the same plant from the median region where, for long distances, the tapering is very slight. The cellular structure corresponds entirely with that in *Dictyostelium*.

In the extreme apical region within the sorus the tapering may become irregular and there may be a slight thickening, the cells becoming disk-shaped instead of vertically elongated as they are a little further back. This is well shown in figure 37. The morphallactic form adjustments of the cells are obviously less perfectly worked out as the process of building the stipe upward comes to a close, under the influence of the limiting factors resulting from the difficulty in maintaining the cell adjustments called for by the growing height and unsteadiness of the whole sorocarp system. A similar tendency to a failure of the morphallactic cellular responses at the apex of the stipe is seen in *Dictyostelium* (1926, pl. 8, fig. 31) but hardly to the degree that it is in evidence in *Polysphondylium*.

The form of the lateral stipes and their relations to each other and to the main axis can be seen in flattened out water mounts of the sorocarps. As noted, they are in the general method of their formation miniature replicas of the main stipe. The stipes of the branches taper much more rapidly than does the main axis, so that they may be quite club-shaped, as shown in figures 38 and 39. In these two figures, and in figure 41, the base of the branch is thicker than the main stipe at that point. In these water mounts the anchoring slime around the bases of the branches shows not at all or very faintly. The change in form of the cells, from isodiametric polyhedra at the base of the branch to flattened disks in the middle, and more or less elongated

cylinders toward the apex of these larger branches, is a very striking exhibition of adaptive morphogenetic determination, (figs. 38, 41, 43 and 44).

The apical load carried by the lateral stipe diminishes progressively as the cells of the sorogen metamorphose themselves into cells of the stipe and presumably lose weight by drying and destructive metabolism. The stipe must of course carry its own weight as well as the weight of the sorus and considered as a static system the bending moment decreases from its base to its apex.

In the basal portions of these branch stipes, formed while the lateral sorogen is still supported largely by direct adhesion to the main stipe, the outlines tend possibly to be more irregular and the taper less even, as is seen in figures 38, 39 and 41. The variations in size of the branches, both as to length, diameter at base, and rate of tapering, are well shown in figures 38-44. There is no doubt a correlation of these stipe dimensions with the size of the lateral sori. As I have noted, the ratio of diameter of sori to length of supporting stipe is 1:2.5 for the lateral branches, and 1:4.5 for the terminal segment and its sorus. Branches may be not more than one cell in diameter from base to apex (figs. 44 and 45) and in such cases the cells change from thin flattened disks (in some cases twice as wide as high) to isodiametric segments of cylinders and, towards the apex, to forms two or three times as long as they are wide (fig. 44.) I have given data as to the changing relations of width and length of the cells in the stipes of *Dictyostelium* (1926, p. 253). The morphallactic adjustments by which these changes in the rate of tapering are brought about are much more accentuated in the branches of *Polysphondylium,* which taper so much more rapidly. The end cell or cells which are enclosed within the sorus, as in the case of the terminal sorus, may be in some cases less tapering or even somewhat thickened.

The rate of taper in the stipes with strongly bulbous bases, such as are shown in figures 38 and 39, varies more rapidly in the basal region and is much more even in the region beyond the first quarter of the total length. If we divide the whole length of such a lateral stipe into segments, beginning at the base, the variations in the rate of taper in the successive segments can be

measured with such accuracy as the lines in the photograph permit. I have taken for the first segment the distance from the base of the lateral stipe to the point at which it attains its greatest width. The increase in width is relatively very rapid in this region. Beginning at this level of greatest width, I have divided the remainder of the stipe into segments of about equal length and determined the diminution in width for each. Table 2 shows the rate of tapering in a branch with strongly bulbous base, like those in figures 38 and 39, and the corresponding rate in a more slender branch with no markedly bulbous swelling at the base (figs. 43 and 44).

TABLE 2

Rate of taper in two lateral stipes differing in the degree of development of the basal bulb

	A. WITH WELL DEVELOPED BASAL BULB		B. WITH THE BASAL REGION ONLY SLIGHTLY BULBOUS	
	Segment	Rate of taper	Segment	Rate of taper
1	Increase	1 : 6¼	Increase	1 : 1
2	Decrease	1 : 2⅝	Decrease	1 : 6⅔
3	"	1 : 10	"	1 : 20
4	"	1 : 20	"	1 : 40
5	"	1 : 100	"	1 : 40
6	"	0	"	1 : 40
7	"	0	"	1 : 40
8	"	1 : 40		
9	Increase	1 : 40		

As shown for lateral stipe *A*, the rate of taper changes rapidly in the bulbous region, segments one and two. It then narrows less rapidly, segments three, four, and five. In segments six and seven there is no measurable taper. In the ninth segment there is a slight increase in the diameter of the stipe.

As noted in many of the lateral stipes the basal bulb is by no means so strongly developed. In the particular case *B* shown in the table, the rate of taper is practically unchanged from segment four to the apex.

The unit bending stress on a branch diminishes from its base to its apex and its tapering form is an expression of the principle of economy in nature. The diallactic creeping movements of the amoebae in the lateral sorogen and the morphallactic form adjustments by which the lateral stipe is built are all carried out in

progressive order under the influence of the graded differences in bending stress in such a system. The fact that the material for the elongation of the stipe comes from the sorogen, so that the whole system is developed progressively with a continuous change in the relative weight of stipe and sorogen, affords another graded series of changes in the barotropic relations at the focus of morphogenetic activity which may well be assumed to have form determining significance.

Organic regulations. Polysphondylium, like *Dictyostelium,* is favorable material for the study of the processes by which teased up fragments of the pseudoplasmodium build new sorocarps. The process in its essential features is simply one of reorganization or reconstruction, with no regeneration of or substitution for lost parts or repair of injury (reparation). Van Tieghem (1880) reported that when a young plant of *Polysphondylium* is teased or crushed out the amoebae separate and renew their vegetative growth and cell division. Later on they begin sorocarp formation anew.

Olive (1902, p. 471) has described the formation of several fructifications from a single pseudoplasmodium when transferred to a fresh drop of nutrient solution. He does not, however, agree with Van Tieghem that in doing this the myxamoebae pass through a further stage of vegetative growth and reproduction. This disagreement may be due to differences in the age of the sorocarps which were used in the experiments.

The process by which a fragment of a pseudoplasmodium builds a symmetrical new sorocarp is that of specifically oriented creeping movements, ordered translocations of the amoebae, and the molding of the individual amoebae together to form the stipe (soma) and the sori (germ plasm) of a new sorocarp. The stages in the transformation of such a mass of amoebae as one of those shown in figure 55 into the sorocarp shown in figure 57 is strictly a matter of morphogenesis and resulting differentiation without either mass or census growth. Nothing is repaired, nothing is replaced by substitution, nothing is regenerated in any sense implying growth. We thus have before us the processes of morphogenesis and differentiation *per se.* The group of myxamoebae simply starts again as a pseudoplasmodium to form a new sorocarp. In such a new plant, as Van Tieghem emphasized

(1880), there is no reason to suppose that any particular cell reaches a position in the new sorocarp corresponding to that it would have achieved if not disturbed. Young sorocarps with a considerable length of stipe are favorable material for studying these reconstructive powers of the myxamoebae. If such young plants are teased up with needles in a drop of water or dung decoction the fragments begin at once the reconstructive processes. For the case just noted figure 55 shows the appearance of two such small masses of myxamoebae photographed in a hanging drop culture at 10 P.M. (magnification 13). They are irregular in outline and many free myxamoebae are regularly present about such masses though not shown at this magnification. Figure 56 shows the same two masses one hour later, 11 P.M. They have moved together and rounded up somewhat. Twelve and one-half hours later, the next forenoon at about 11:30 A.M., they had each formed sorocarps with branches. The upper one shows a stipe with a whorl of branches midway in its height and a single branch or a more or less distinct simple sorocarp at its base (fig. 57). The lower one of the two was not favorably placed for photographing. It showed a sorocarp with one branch near its base and three other branches or independent sorocarps whose relations to the basal mass were not clear. As noted, free myxamoebae were also present in the culture though not visible with the magnification used in making the photographs.

Figure 52 shows a fragment of a stipe with masses of myxamoebae adhering to it as they appeared in a preparation of a young sorocarp teased up in a hanging drop. The photograph was made at 9 P.M. The preparation was photographed again at 10:15 P.M. and showed the myxamoebae rounded up in three main masses along the stipe (fig. 53). The next morning at 11:30 these masses had formed sorocarps as shown in figure 54: at least eight sori are shown with their stipes extending at various angles from the basal masses. When such small sorocarps stand vertically to the plane of the picture the stipe is hidden by the sorus. The basal residual masses consisting of gelatinous material in which the base of the stipe is embedded are quite rounded, and in some cases appear in the photographs to be nearly as large as the sori. They are less dense, however, and more irregular in outline.

Figure 58 shows another longer portion of a stipe and sorogen which was dragged about in a hanging drop of dung decoction and finally mounted. The myxamoebae are distributed in irregular clumps and masses on the stipe, and are already showing a tendency to form rounded groups. Other masses of amoebae were scattered here and there in the culture and the next morning, twelve hours later, many of them had formed sorocarps and were photographed. The largest clump had made at least six sorocarps, as shown in figure 59. Another clump (fig. 60) had made a single sorocarp with a pair of branches about midway of the stipe. Three others were simple and unbranched and of very unusual proportions, the stripes being in length only two or three times the diameter of the sorus. Figure 61 shows a very diminutive specimen with a pair of apparently abortive branches near the base of the main stipe.

Perhaps the simplest case of these morphogenetic regulations is seen when a young sorocarp is bent over until the sorogen touches the substratum. This happens frequently, and I have described such a case above as it occurred naturally in the development of a sorocarp in a petri dish culture. The results of such an interruption of normal development may be studied and photographed under controlled conditions if a young sorocarp, before branch formation has begun, is picked off the substratum and its tip carefully brought in contact with the agar medium in a fresh hanging drop. The sorogen adheres to the agar, and if left in this position with a minimum of disturbance, proceeds almost at once, with no tendency to preliminary rounding up, to the completion of a sorocarp. The stages in this process are shown in the photographs 46 to 51. These were taken from the same preparation at successive intervals of about fifteen minutes. Figure 46 shows the sorogen and a bit of the stipe of a young sorocarp as it has just been picked up, laid in a drop of water and placed in a moist chamber. A certain number of amoebae escape from such a mass, especially at its apex, but in general they do not appear clearly in the photograph. The trumpet-formed widening of the stipe at its extending apex is shown here as in my figure 14, plate 6 (1926) of *Dictyostelium*. The diagonal line running past the base of the sorogen in the direction of the stipe outlines the boundary of the slime deposited in the process of laying

down the sorogen. The position of this line with relation to the sorogen in the succeeding figures is a good index of the movement of the latter.

Figure 47 is from a photograph taken fifteen minutes later; the apical region of the sorogen has already begun to curve upward without any noticeable antecedent rounding up or change of outlines. The mass has, however, pushed forward and added to the length of the stipe, as is shown by the position of its base in relation to the end of the dark line of amoebae lying along the earlier formed part of the stipe and the relative position of the slime line referred to above.

That the sorogen is curving upward is shown by the dark anterior zone, due to stoppage of the light, the high light on the apex, and the fact that the sorogen as seen from above appears shorter by the amount that it has curved upward. The relations of the parts and the nature of the process would be better shown in a photograph taken from the side but I have not been able, without disturbing it too much, to get a sorogen in position for such a picture.

Figure 48 shows what occurred in the next fifteen minute interval. The upturn of the apex has proceeded still further so that the length of the horizontal part is only about one-half what it was when the experiment began. The further forward movement of the base is shown in relation to the reference points noted above. In this figure the nature of the sorogen as a mass of free amoebae is indicated by the fact that certain of the amoebae have become separated from the mass and are left behind along the stipe. Other amoebae are seen bulging from its sides.

Fifteen minutes later, as shown in figure 49, the sorogen has come to stand almost vertically on end and the basal portion appears much more tapering. The outline of the stipe can be traced, forming the axis of the mass, and the high light spot marks its vertex. In another fifteen minutes (fig. 50) the sorogen has practically regained its position vertical to the substratum. For this figure the negative was exposed at a higher focus and the free amoebae in the culture medium appear as high light spots, etc., due to their being out of focus. In figure 51 the sorogen appears in end view merely as a rounded black mass.

The process by which the pseudoplasmodial mass erects itself

in this case simulates that by which a root or shoot regains its normal geotropic relations when laid in a horizontal position. This latter process has long been known to be a growth curvature. In the case of the young sorocarp there is no growth either in mass or number of cells. As noted, some cells may drop behind in the process, and there is doubtless loss of weight, due in part to destructive metabolism involved in the work done. The stimuli which initiate and direct the reaction are doubtless hygro- and geotropic, and the process is one of specifically oriented motion, the anallactic creeping of the mass of myxamoebae. The sorogen bends upward like a shoot, but the bending is due to the specifically oriented direction of creeping of the myxamoebae. The facts are unmistakable. If, as in the ordinary class experiment to show the growth curvature of a root, you were to lay off on the sorogen of *Polysphondylium* a series of lines at equal distances apart, these distances would not be changed while the curvature was taking place, barring possible slight differences between the convex and concave flanks due to shifting of their position by the individual amoebae.

The recovery of the erect position by the sorogen of *Polysphondylium* is not a growth curvature, and in the light of the facts here we may well question whether specifically oriented tropistic movements involving mass growth and cell multiplication in the root and shoot should not be regarded as determined by intercellular relations analogous to those existing between the free amoebae in the sorogen, rather than by some organismal principle of root or shoot behavior. In both cases the external stimuli of gravity, relative moisture, etc., are the same.

In *Polysphondylium* mass growth is completed in the free swarming stage and is unoriented. The myxamoeba enlarges in three dimensions. Whether division is oriented in the sense that the planes of successive bipartitions would intersect at right angles as in *Pediastrum* is not determined. In any case a specific orientation of the division planes would mean nothing for the organization of the future sorocarp, unless some sort of pattern orientation is assumed to be maintained by the amoebae in all their wanderings and then to further determine their arrangement in the process of stipe and sorus formation, which is scarcely conceivable.

Discussion. When in *Polysphondylium* unoriented mass growth and unoriented census growth have been completed and the myxamoebae have reached what we call the maturity of the fruiting stage, specifically oriented movements begin. Differentiations based in each case on specific positions successively achieved by the cells emerge and lead to the formation of the sorocarp with its definitely oriented position with relation to the substratum, the more or less fixed size relations between its parts, its radial and metameric symmetry, and differentiation into soma and germ plasm. For *Polysphondylium* it is obvious that growth and differentiation, instead of being expressions of an organismal protoplastic mass, are respectively the processes of cell growth and cell multiplication followed by cell aggregation and cell differentiation in a colony whose unity and organization are matters of specialization in position and function, worked out by the interactions of its component cells.

In the case of the Myxomycetes we have in the true plasmodium an organized mass of protoplasm which, by specifically regulated movements as a mass, may produce stalked fruit bodies quite similar to those of the Acrasieae. However, differentiation never proceeds as far in the Myxomycetes as in the sorocarp of *Polysphondylium* with its whorls of branches and its sharp differentiation of soma and germ plasm. A comparison of the organization of *Stemonitis* with that of *Polysphondylium* shows at once the greater possibilities which go with the colony of free individual cells, as contrasted with the multinucleated protoplasmic mass of *Stemonitis*. The latter is, as I have elsewhere pointed out, functionally, in its reactions and capacity for differentiation, a single cell. Its stipe and capillitial system are secretions. It shows no metamerism nor differentiation of soma and germ plasm. To be sure such coenocytic algae as *Bryopsis* and *Caulerpa* show more complexity of form than does *Polysphondylium*, but that they are at a disadvantage in their capacity to achieve complexity and specialization in organization, as compared with true multicellular plants such as the red algae, will hardly be denied. To claim that, after all, the plant is only a mass of protoplasm, whether cut up into cells or not, is to overlook the obvious facts of organization in the Myxomycetes and Siphoneae as compared with the red or

brown algae and the higher plants, in which the unit of organization and differentiation is in general the uninucleated cell.

Morphogenesis and differentiation in *Polysphondylium* involve cellular phenomena of at least three types: (1) Translocatory, in turn synallactic, anallactic, and diallactic amoeboid creeping movements, by which the pseudoplasmodial mass is formed from the free creeping amoebae and further transforms itself into the mature plant, the sorocarp, with its polar differentiation, its metameric and radial symmetry, and its apical and lateral sori. (2) Specific morphallactic cellular form adjustments at the ends of the elongating stipe and branches, by which the myxamoebae fit themselves together so as to achieve the tapering columnar form of the stipe and branches with their curves and angles adapted to support and maintain the equilibrium of the load of sori. (3) Intracellular histogenetic metamorphoses of the cells *in situ*, in the stipe and in the sori respectively, by which they become vacuolar, expand and become closely pressed together into a parenchyma-like tissue in the stipe and take on the oblong form with dense contents of the spores in the sori.

The third of these phases is the same in principle in these semi-coenobes as in the metaphytes, though, in the latter of course a vastly longer list of tissues is produced. The first generally recognized change in the cells, as you proceed backward from the apical region of a root tip, is vacuolization of the cytoplasm as a simple method of cell enlargement, and Olive has emphasized and made very clear the part which vacuolization plays in the differentiation and enlargement of the stipe cells in these Acrasieae. He has also given in detail the evidence for the development of specialization of the wall in the cells of the stipe, which is also a main factor in the differentiation of the vascular and strengthening tissues in the metaphytes.

The second type of cell changes in these semi-coenobes—the morphallactic form adjustments at the tips of the stipe and branches by which the tapering form of the stipe is achieved and the direction of elongation is so controlled as to maintain the equilibrium of the top-heavy mass and develop the smooth curves and balanced form which is so characteristic—is apparently the most specific for this type of plant. The general adaptive signi-

ficance of the erect and branching habit of *Polysphondylium* is plainly that of securing better distribution of the spores. The Sorophoreae, as both Olive's work and that of earlier students of the group has shown, present a well defined evolutionary series of types in which elevation of the sori above the substratum is obviously a factor of high selective value. The reversal of the hygrotropic relations of the species as they pass from the vegetative myxamoeboid stage to that of maturity and spore dissemination is a long known fact for the group.

Parr (1926) has attempted to bring greater clarity into the discussion of adaptations by pointing out that adaptation is a relation between an organism and its environment, rather than a character of either the organism or its environment. However this question of verbal usage may be, the adaptive relation for spore dissemination is plainly an achievement, both in the phylogeny of the group and in the species, worked out by the specific reactions of the myxamoebae to their environment. The development of the series is highly adaptiogenetic rather than simply orthogenetic, and the interrelations of form and function are well illustrated. Of more theoretic interest perhaps is the fact that in this process of aggregation and differentiation we have in very simple form an example of the nature of integration and organization by which out of a manifold of unit individuals an individual of another order arises.

To many it would appear that we have no adequate working hypothesis as to the nature of somatic segregation and differentiation. Granting the genic transmission of the *Anlage* for the characters of adult plants and animals we are still wholly at a loss to account for the working out and expression of these characters in ontogeny (Lillie, 1927.)

Heidenhain (1923) feels that the development of the cell theory has resulted only in an analysis of the biological problem, and that further progress must involve attempts at least at synthesis. From this standpoint he has developed his conception of the biosystems, briefly: (1) centrioles, chromioles, etc.; (2) chromosomes, etc.; (3) nuclei; (4) cells; (5) muscles, nerves, etc.; (6) units of symmetry, metameres, antimeres, etc. The development of *Polysphondylium* may be well expressed in terms of such a series, and it further shows that the successive transitions in such

an ascending scale are achieved in each instance by the integrating activity of the cells themselves.

Whether Bertalanffy (1928), with his postulated immanent biologic factors for form, has escaped the vicious circle of neovitalism may be a matter of dispute. The obvious fact as to *Polysphondylium* is that we have in its development a case of integration, in which the manifold (the swarm of amoebae) emerges into the unity of a higher order as an expression of the interrelated and coördinated activities of the cell units. The form determining moments or organizing principles, if such there be, reside obviously in the myxamoebae rather than in the erect, axially elongated, metameric and radially differentiated and symmetrical sorocarp.

It is to be hoped that Bertalanffy will soon give us the further part of his analysis which he suggests (p. 213) and which is to deal with the morphogenetic significance of the hormones and other agencies of chemical interrelations between cells, tissues, and organs, as well as the effects of nerve stimuli, functional activity, etc. Bertalanffy excuses this omission partly on the ground that he is first concerned with the ultimate and 'primary form building processes' and that these chemical and other interrelations in the organism are essentially matters of functional coördination which, as it were, presuppose organization. In the last analysis morphogenesis, aside from differentiation, in the metaphytes is a matter of specifically oriented cell enlargement and specifically oriented cell divisions, however they may be determined. That hormones do determine such processes in many cases is becoming more and more clear, as well as the fact that growth stuffs may determine tropistic curvatures. One can hardly question that the problems of form development in these semi-coenobes appear in relatively simple form and that the organization achieved in the sorocarp is in its structural constitution simple and primary for plants. The sorocarp of *Polysphondylium*, with its erect tapering stem, branches, and fruits, is as it were a diagram of the cormophyte as seen in ferns and seed plants. That, however, chemical interrelations between the cells are basic for the synallactic aggregation stages in *Polysphondylium* seems to be a natural assumption. Chemical stimuli may be also involved as well as contact, pressure, and weight rela-

tions in the morphallactic cell adjustments by which the stipe and branches are built and the general equilibrium of the sorocarp is maintained.

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Explanation of plates 5-9

All the figures are of *Polysphondylium violaceum* Bref., and the photographs were made with the Zeiss apochromatic objectives and compensating oculars and the Zeiss microplanars.

PLATE 5

Figures to show general habit and variation in size and proportions. Magnification about 50 diameters except as noted.

Figs. 1, 2. Unbranched sorocarps like those of *Dictyostelium*.

Fig. 3. Sorocarp with a single branch.

Fig. 4. Sorocarp with single lateral sorus with no stipe or a very short stipe.

Fig. 5. Sorocarp with one whorl of three branches.

Fig. 6. Two sorocarps very close together at base. The one to the right unbranched, the other with a single whorl of three branches placed unusually close to the terminal sorus. The figure also shows at the lower right hand corner a single sorus and part of the stipe of another plant.

Fig. 7. Sorocarp with whorl of three branches and at the node above a single branch.

Fig. 8. Sorocarp with whorl of three, and one with whorl of two branches. Internode unusually short.

Fig. 9. Sorocarp with two whorls of four branches each.

Fig. 10. Rather normally proportioned sorocarp with two whorls, one with four and one with three branches.

Fig. 11. Sorocarp with five whorls of branches.

Fig. 12. Sorocarp with eight whorls of branches. Number of branches per whorl varies from one to six.

Fig. 13. Sorocarp with eight whorls of branches. × about 60.

Figs. 14, 15. Two sorocarps each with seven whorls of branches. × about 20.

Fig. 16. Sorocarp with eleven whorls of branches, with from two to four branches per whorl. × about 20.

PLATE 6

Myxamoebae and stages of aggregation to form the pseudoplasmodium. Figs. 17 and 18 with apochromatic objective 8 mm., compensating ocular 12. Figs. 19-22 microplanar 3.5 cm.

Fig. 17. Myxamoebae in free swarming stage, movement rather sluggish. Exposure 5 sec. × about 400.

Fig. 18. Myxamoebae more active, tending to elongate. Exposure 5 sec. × about 375.

Fig. 19. Central region of a pseudoplasmodium showing synallactic flowage to a center at which a sorocarp is to be formed. × about 40.

Figs. 20, 21. A later stage of development of the same pseudoplasmodium, in which the young sorocarp shows in the photograph as a blunt projection from the central mass. Figure 21 is more highly magnified and was taken only a few minutes later.

Fig. 22. Young sorocarp arising from a rather one-sided pseudoplasmodium. The dark line extending diagonally across the figure is the basal portion of the stipe of another sorocarp.

PLATE 7

Young sorocarps showing anallactic upward movement and diallactic plagiotropic branch formation. Photographed with microplanar 3.5 cm.

Fig. 23. Young sorocarp. Stipe about twice the length of the sorogen.

Figs. 24, 25, 26. Three stages in development of same sorocarp, showing successive abstriction of segmental masses from the apical sorogen.

Figs. 27-31. Four stages in branch formation of the same sorocarp. Photographs taken at intervals of ten to twenty minutes. At the same time the apical sorogen has bent over until it touched the substratum, and then changed its direction of motion and begun to regain its position vertical to the substratum.

Figs. 32, 33, and 34 show various stages in the development of the segmental masses into whorls of branches.

PLATE 8

The formation of the stipe and branches. All figures taken with the Zeiss 8 mm. objective and compensating ocular 12.

Fig. 35. Base of stipe irregular in outline and turned to one side.

Fig. 36. Segment of same stipe in median region; tapering slight.

Fig. 37. Apical segment of a stipe showing slight thickening where enclosed in the terminal sorus.

Fig. 38. Lateral stipe with strongly bulbous base.

Fig. 39, 40, 41, 43. Lateral stipes with less bulbous swelling at base.

Fig. 42. Shows one complete lateral stipe and the bases of two others in the same whorl.

Fig. 44. Shows a lateral stipe consisting of a single row of cells. The tapering is determined entirely by the form of the cells.

Fig. 45. Shows the bases of three branches in a whorl with different degrees of bulbous enlargement.

PLATE 9

Illustrations of organic regulations in *Polysphondylium*. Figures 52 to 60 were made with Zeiss microplanar 3.5 cm.

Figs. 46-51 show stages by which the sorogen of a young sorocarp when laid horizontal on the substratum turns up by anallaxis until it has regained the vertical position. The pictures were taken with Zeiss apochromatic objective 16 mm. compensating ocular 8, at intervals of about fifteen minutes.

Fig. 52. Fragment of stipe with amoebae adhering to it from young sorocarp teased up and mounted in hanging drop.

Fig. 53. The same preparation after about seventy-five minutes.

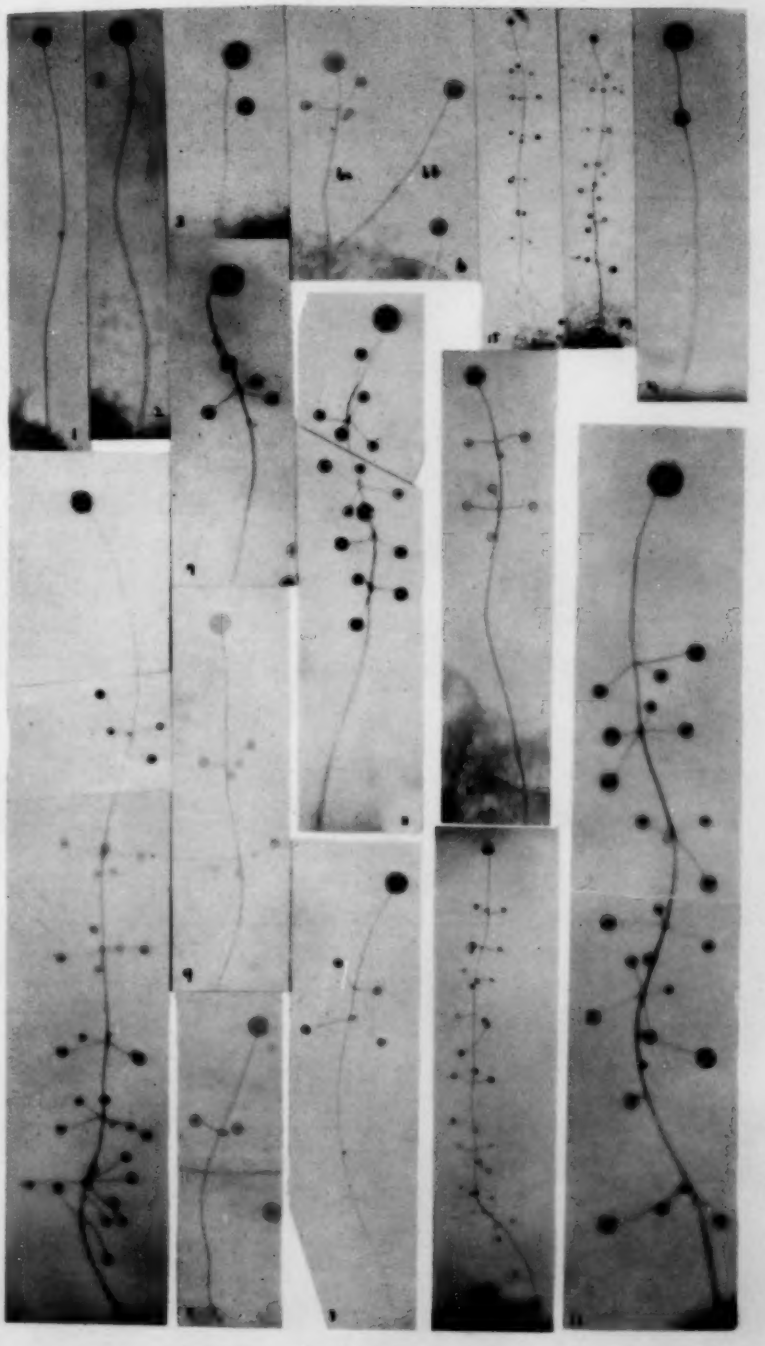
Fig. 54. The same preparation after about fourteen hours.

Fig. 55. Two masses of amoebae teased off from a young sorocarp.

Fig. 56. The same one hour later.

Fig. 57. One of two sorocarps formed during the next twelve hours from the upper one of the masses of amoebae shown in the two previous figures.

Figs. 58-61. A similar series to that shown in figures 52-54.



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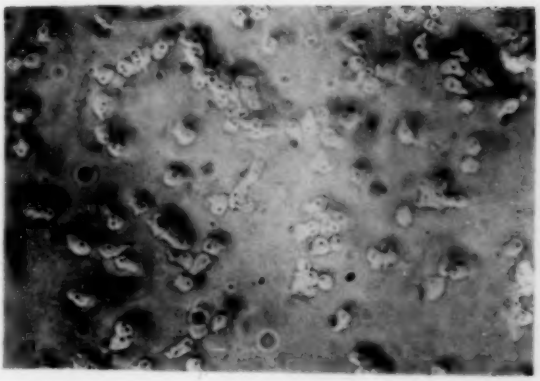

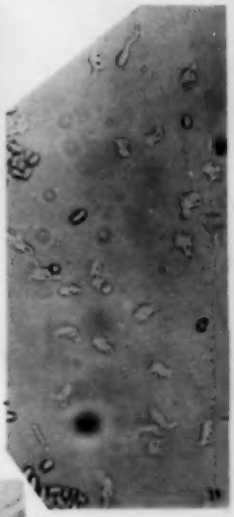

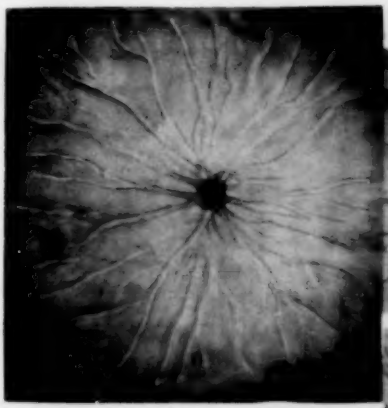

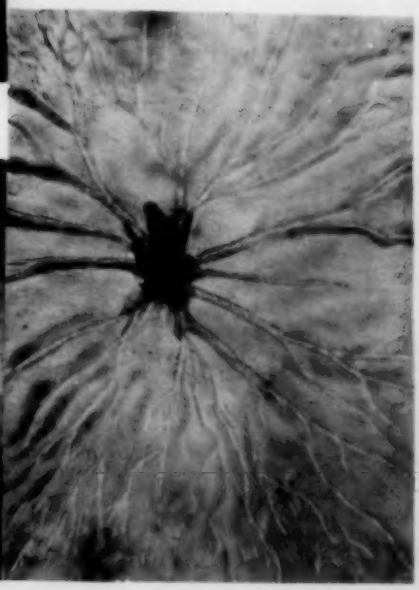

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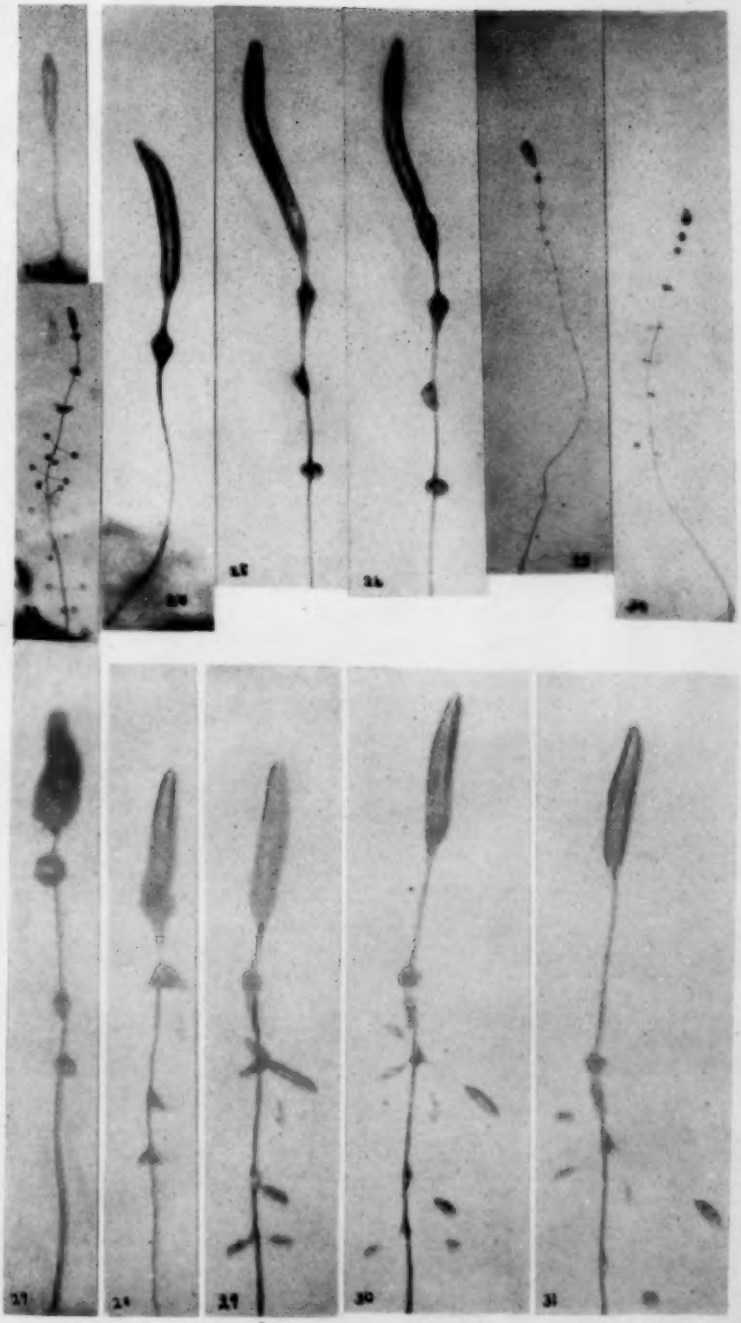

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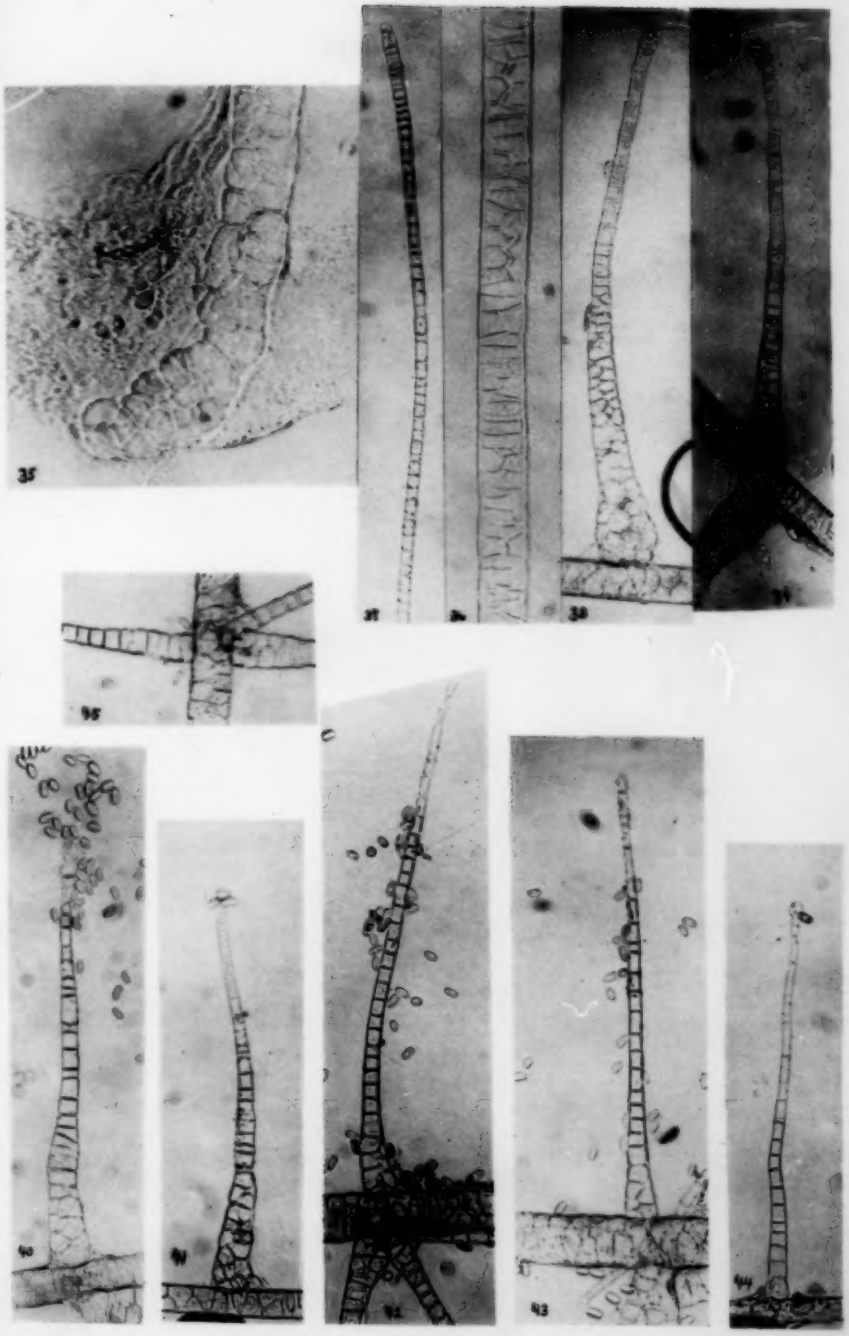

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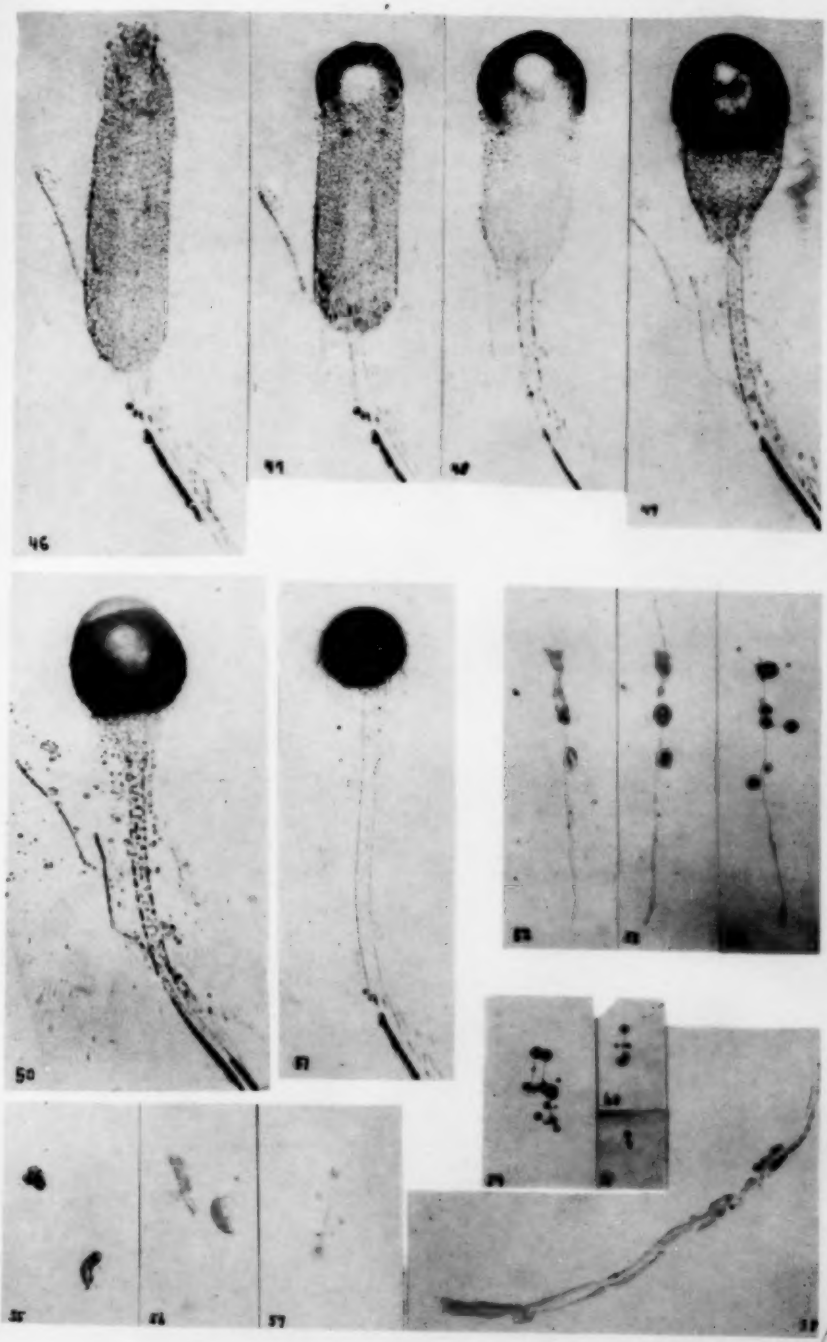
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Histology of the wood of angiosperms

I. The nature of the pitting between tracheary and parenchymatous elements

FREDERICK H. FROST[1]

(WITH PLATE 10)

During the course of an investigation of the structure of the wood of our native arborescent angiosperms the writer has observed several features which warrant separate treatment. The type of pitting found when a vessel segment, tracheid, or fiber lies adjacent to a xylem parenchyma or ray parenchyma cell will be discussed in this instance.

The following quotation from Solereder (6) summarizes the present status of opinion in respect to this point.

> These walls (walls of contact between a vessel segment and a parenchymatous cell) are occupied (a) either by one-sided bordered pits (half-bordered in the common terminology) one or more[2] of which corresponds to large one-sided simple pits on the adjoining parenchyma-wall, or (b) by one-sided simple pits of varying size which correspond to pits of equal dimensions on the wall of the adjoining parenchyma cell.

In other words, the wall of a parenchymatous cell in this situation possesses simple pits, while the vessel wall may have either bordered or simple pits. Similar statements may be found in the classical texts of Strasburger (7), De Bary (1), or Haberlandt (3), in the more recent texts such as Eames and MacDaniels (2), or Jeffrey (4), and in works dealing with the detailed structure of wood, such as Record (5).

It is undoubtedly due to the very concise statements of the above investigators that a thorough study of these pits has not been made and their true nature described in detail.

MATERIALS AND METHODS

The sections used in this investigation average about five microns in thickness and were stained *lightly* in Haidenhain's iron-alum haematoxylin and safranin. It is essential, if the de-

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[2] See figures 1, 2. This condition is due to the breaking up of scalariform pitting into opposite pitting and is common in species with scalariform perforations.

tails of the pitting are to be clear, that the staining is light and that both the haematoxylin and safranin are destained. The wood was softened with hydrofluoric acid but was not embedded. Properly softened wood will nearly always cut as thin as five microns if the microtone knife is in excellent condition. The nature of the pitting was, of course, determined in section, as it is impossible, in most cases, to distinguish between a half-bordered pit and a fully bordered pit in face view.

OBSERVATIONS AND DISCUSSION

It is an almost universal rule that the same type of pitting exists, in a given species, between the ray parenchyma and tracheary elements and xylem parenchyma and tracheary elements. For this reason the discussion which follows applies to both ray and xylem parenchyma.

The pitting of vascular parenchyma[3] cells, when adjacent to vessel segments, falls into four main groups as regards the outline of the pits in face view. These pits may be scalariform, as in *Gordonia lasianthus* Ellis (fig. 1) and many other primitive woods; reticulate, which is transitional between the scalariform and opposite types, as is found occasionally in *Sambucus Simpsonii* Rehder (fig. 2); opposite, as is frequently the case in *Carpinus caroliniana* Walter (fig. 3); or alternate, as is well illustrated in *Acer floridanum* (Chapman) Pax (fig. 4).

In section the vessel-vascular parenchyma pits, when scalariform in face view, are very often fully bordered. This condition is typical of *Gordonia lasianthus* Ellis (figs. 5, 6) and *Liquidamber styraciflua* Linnaeus (fig. 13). The scalariform-half-bordered condition is shown very clearly in *Symplocos chiriquensis* Brand (fig. 7). Scalariform simple pits are, as one would expect, quite rare, and if found are usually associated with half-bordered pits or fully bordered pits. Figure 8 illustrates these pits from *Anacardium excelsum* Skeels.

The reticulate or intermediate type of pitting may be fully bordered, half-bordered, or simple. Illustrations of these types may be found, in the same order as above, in the following species: *Magnolia acuminata* Linnaeus in part, *Dalea spinosa* Gray,

[3] The term 'vascular parenchyma' is here used to denote both ray and xylem parenchyma.

and the reticulate simple pits occasionally occur in *Trema mollis* Loureiro. In the latter species the pits are usually one-half bordered.

Likewise the opposite or alternate type of pitting may be fully bordered, half-bordered, or simple. Excellent bordered pits of these two types may be found in *Ostrya Knowltonii* Coville (fig. 9, a, b). Very distinct half-bordered pits occur in *Hicoria pecan* Britton (fig. 10), and simple pits are quite common in *Sambucus coerulea* Rafinesque (fig. 11).

The writer has observed bordered pits in parenchymatous cells in a number of other genera, both tropical and temperate, and it is certain that the occurrence of these types are not abnormalities,[4] but are consistent features of the structural elements of wood. The sequence of changes which these pits undergo during the course of evolutionary specialization will be treated in detail in a later paper.

The pitting between parenchymatous elements and fibers is not abundant and the pits are generally small. Pits between libriform fibers (libriform fibers have simple inter-fiber pits) and parenchyma cells are always simple (fig. 16, *Sambucus callicarpa* Greene). Pits between tracheids or fiber tracheids and parenchyma cells, on the other hand, may be bordered, half-bordered, or simple, since the inter-fiber pits are always bordered.

Bordered pits in this situation are found quite frequently and are very clear in thin and properly stained preparations of *Gordonia lasianthus* Ellis (fig. 12), *Platanus Wrightii* S. Watson, and *Liquidamber styraciflua* Linnaeus (fig. 13). The half-bordered pit is quite common and is illustrated by *Malus coronaria* Miller (fig. 14). The simple type is found in *Betula lenta* Linnaeus (fig. 15) with the half-bordered type. The writer has not observed simple pits in this situation in woods which possess fibers with well developed bordered inter-fiber pits.

From the foregoing notes and the writer's observations it is clear that the type of pitting between a tracheary element and parenchymatous element is determined to a large extent by the degree of specialization of the tracheary element rather than the

[4] Thompson, W. P., Bot. Gaz. **53**: 331-358, describes and figures a ray parenchyma cell from *Abies* with bordered and simple pits. Cells of this type have also been described from *Sequoia*.

parenchymatous element. Exceptions to this rule occur in groups which posses the heterogeneous type of ray, in which cases the upright ray parenchyma cells often show a different type of pitting than the radially elongate ray parenchyma elements.

The details of pitting, of the types above described, are useful in wood identification studies, since they increase the number of possible characteristics a plant may possess. In transitional genera, such as *Sambucus,* it is possible to differentiate easily between certain species by the occurrence of bordered or simple vessel-ray pits.

It is likewise possible to distinguish between the North American species of *Ostrya* and *Betula* on the basis of the pitting between fibers and xylem parenchyma, but in closely related genera like *Liriodendron* and *Magnolia* or *Salix* and *Populus* the details of the pittings are usually identical. The type of vessel-ray or fiber-parenchyma pitting as a rule is more apt to be characteristic of a subfamily or family than of the individual species of a genus in our native arborescent angiosperms.

SUMMARY

1. The prevalent conception of the type of pitting which occurs between tracheary and parenchymatous elements in the secondary xylem of angiosperms is incorrect.

2. Fully bordered, half-bordered, and simple pits are characteristic features between tracheary cells and vascular parenchyma.

3. The type of pitting on the wall of the parenchyma cell is controlled largely by the degree of specialization of the vessel or fiber which lies next to it.

4. The detailed structure of pits of this nature is useful in wood identification.

In conclusion the writer wishes to express his appreciation to Professor I. W. Bailey for many kindnesses.

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Explanation of plate 10

(*v.s.* refers to vessel segment; *x.p.* to xylem parenchyma; *r.p.* to ray parenchyma; and *t.* to tracheids or to fibers.)

Fig. 1. *Gordonia lasianthus.* Scalariform vessel-ray pits. Radial Section.

Fig. 2. *Sambucus Simpsonii.* Reticulate vessel-ray pits. Radial section.

Fig. 3. *Carpinus caroliniana.* Opposite vessel-ray pits. Radial section.

Fig. 4. *Acer floridanum.* Alternate vessel-ray pits. Radial section.

Fig. 5. *Gordonia lasianthus.* Bordered fiber-ray and fiber-parenchyma pits. Scalariform bordered vessel-parenchyma pits. Transverse section.

Fig. 6. *Gordonia lasianthus.* Scalariform bordered vessel-ray pits. Tangential section.

Fig. 7. *Symplocos chiriquensis.* Scalariform half-bordered vessel-ray pits. Tangential section.

Fig. 8. *Anacardium excelsum.* Scalariform simple vessel-ray pits. Tangential section.

Fig. 9. *Ostyra Knowltonii.* (a) Opposite bordered vessel-parenchyma pits. (b) Opposite bordered vessel-ray pits. Radial and tangential section.

Fig. 10. *Hicoria pecan.* Opposite half-bordered vessel-ray pits. Tangential section.

Fig. 11. *Sambucus coerulea.* Alternate simple vessel-ray pits. Tangential section.

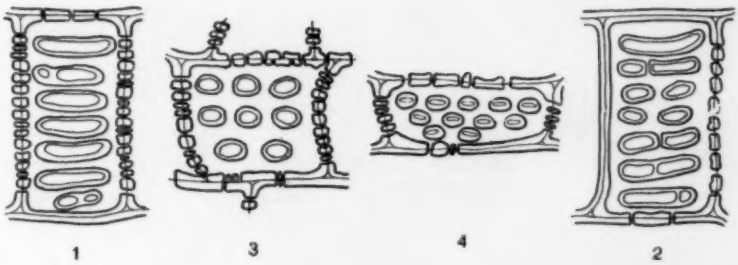
Fig. 12. *Gordonia lasianthus.* Bordered fiber-parenchyma pits. Radial section.

Fig. 13. *Liquidamber styraciflua.* Bordered fiber-ray pits and scalariform bordered vessel-ray pits in the same cell. Tangential section.

Fig. 14. *Malus coronaria.* Half-bordered fiber-parenchyma pits. Radial section.

Fig. 15. *Betula lenta.* Simple fiber-parenchyma pits. Radial section.

Fig. 16. *Sambucus callicarpa.* Simple pits between libriform fiber and xylem parenchyma. Radial section.



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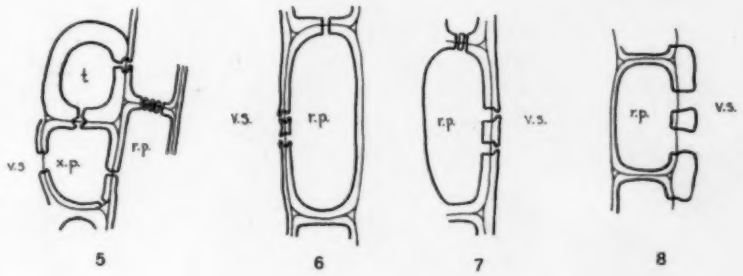

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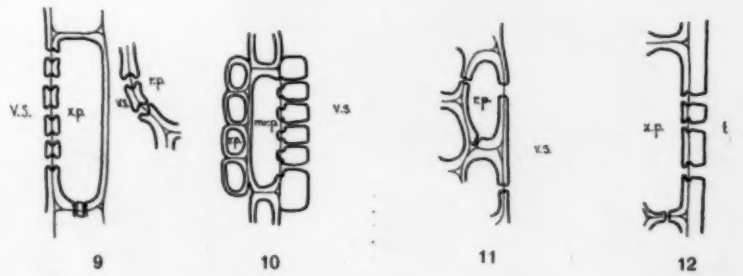

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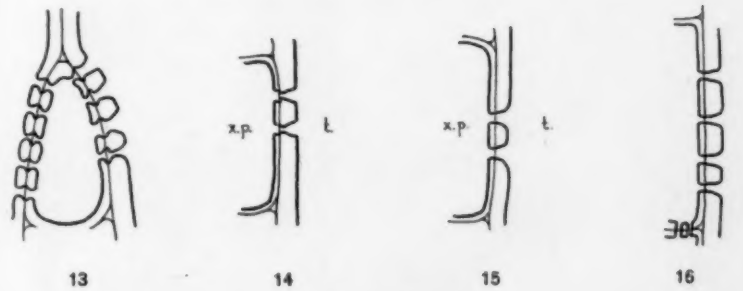

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FROST: WOOD OF ANGIOSPERMS

The genus Viburnum in northwestern South America

E. P. Killip and A. C. Smith

In attempting to identify a large series of specimens of *Viburnum* which we collected in eastern Colombia, we found that nearly all the Andean material of this genus in American herbaria had been referred to *V. glabratum* H.B.K., though quite obviously several species were represented. Monographers apparently have paid little attention to the South American representatives of the genus, confining themselves almost wholly to the species occurring in the North Temperate regions. Several Peruvian species were recently described by Graebner, but these appear to be local species which do not range into the northern part of the Andes.

As in the case of the species from North America and the Old World, the principal diagnostic characters lie in leaf-shape, indument, and size and branching of the corymbs, the flowers and fruits showing little variation.

The herbaria in which specimens we have examined are deposited are indicated thus: Arnold Arboretum (A); Field Museum of Natural History (F); Gray Herbarium of Harvard University (G); Royal Botanic Gardens, Kew (K); U. S. National Herbarium (N); New York Botanical Garden (Y).

KEY TO SPECIES

Lower surface of leaves uniformly pubescent with stellate hairs, usually at least 5 per sq. mm. of surface on mature leaves.

Leaf hairs straight (.3-.6 mm. long); corymbs wide-spreading, more than 8 cm. wide, often 13 cm.....1. *V. lasiophyllum.*

Leaf hairs crispate (.15-.3 mm. long); corymbs smaller, rarely more than 10 cm. wide, usually less than 8 cm.

Plants of lax habit, with elongate branches; inflorescence 3- or 4-times branched; leaves rarely in threes.....2. *V. pichinchense.*

Plants compact, the branches short; inflorescence twice-branched; leaves often in threes.....2a. *V. pichinchense toledense.*

Lower surface of leaves essentially glabrous, sometimes pilosulous in axils of nerves.

Branchlets and rays of inflorescence densely canescent-pulverulent. 3. *V. glabratum.*

Branchlets and rays of inflorescence glabrous or with various indument, not pulverulent.

Leaves thick coriaceous, often in threes.....4. *V. triphyllum.*

Leaves herbaceous, never in threes.
Leaves broadest above the middle.
Branchlets essentially glabrous; petioles about 15 mm. long; bractlets persistent, up to 7 mm long; calyx tube densely glandular-punctate. .....5. *V. apiculatum.*
Branchlets rufo-tomentose; petioles less than 10 mm. long; bractlets deciduous, about 2 mm. long; calyx tube sparingly glandular-punctate. .....6. *V. suratense.*
Leaves broadest below or near the middle.
Leaf margins slightly revolute and appearing to be regularly ciliate. .....7. *V. fragile.*
Leaf margins flat and obviously not ciliate.
Apex of leaves obtuse (rarely obtusely acuminate).
Branchlets and rays of inflorescence glabrous or sparingly appressed-hirtellous, bractlets about 3 mm. long.
Leaves more than 7 cm. long; texture herbaceous....
8. *V. leptophyllum.*
Leaves less than 7 cm. long; texture thin herbaceous.
8a. *V. leptophyllum venezuelense.*
Branchlets and rays of inflorescence densely rufo-tomentose with matted hairs; bractlets about 1.5 mm. long.
Corymbs less than 10 cm. wide, the rays straight, stout, ascending; branchlets stout. .....9. *V. floccosum.*
Corymbs more than 10 cm. wide, the rays flexuose, slender, divaricate; branchlets slender.....10. *V. divaricatum.*
Apex of leaves sharp-acuminate or long-acuminate.
Leaves twice as long as broad.
Corymbs ebracteate and ebracteolate; calyx lobes semicircular, finely and regularly ciliate.....11. *V. cornifolium.*
Corymbs deciduously bracteate and bracteolate; calyx lobes ovate, smooth at the margins or slightly ciliate.
12. *V. Lehmannii.*
Leaves three times as long as broad .....13. *V. Toronis.*

DESCRIPTIONS OF SPECIES

1. VIBURNUM LASIOPHYLLUM Benth. Pl. Hartw. 189. 1845. Shrub 3-4-m. high; branchlets subterete, densely and softly stellate-ferruginous-tomentose, the internodes 4-7 cm. long; petioles 8-13 mm. long; leaves broadly ovate or oblong-ovate, 4-7 cm. long, 3-6 cm. wide, acute or abruptly acuminate at apex, subcordate at base, obscurely sinuate-dentate or subentire in upper half, entire in lower half, stellate-pubescent with straight hairs (.3-.5 mm. long), the pubescence much denser and softer beneath, the nerves scarcely impressed above; corymbs sessile or pedunculate, 8-12 cm. wide, pubescent as the branchlets, bracteate with soon deciduous linear

bracts (about 5 mm. long), 5-8-rayed (primary branches 2-4 cm. long), 3- or 4-times branched, bracteolate, the bractlets linear-oblong, 3-4 mm. long, persistent; calyx tube about 1.5 mm. long, sparingly glandular-punctate and pubescent with scattered short stiff hairs, the lobes triangular, about 1 mm. long, subacute, strongly ciliate; corolla about 2 mm. in diameter at the base, 3-4 mm. long, the lobes oblong-ovate, 2 mm. wide; ovary furrowed.

COLOMBIA: Cundinamarca: Pacho, *Hartweg 1041* (type; N, fragment and photo; Y, photo). Other specimens are: *Pennell 2474* (Y), from Sibaté, and *Appollinaire & Arthur 76* (N), from Gaudalupe, both in the same general locality as the type, which differ in having proportionately narrower leaf blades with petioles less than 5 mm. long.

2. V. PICHINCHENSE Benth. Pl. Hartw. 188. 1845. *V. Urbani* Graebn. Bot. Jahrb. **37**: 435. 1906. Shrub 2.5 to 4 m. high, much branched, the branches elongate, up to 8 meters long; branchlets and rays of inflorescence ferruginous-stellate-tomentose with crispate tangled or matted hairs .15-.3 mm. long; petioles .5-1.5 cm. long; leaves ovate, oblong, or slightly obovate, 8-12 cm. long, 4-6 cm. wide, acute or abruptly acuminate at apex, rounded at base, entire or subentire, impressed-nerved and sparingly stellate-pubescent above, rufo-stellate-tomentose beneath, the hairs like those of the branchlets; corymbs pedunculate, 4-7 cm. wide (occasionally up to 9 cm.), ebracteate (or sometimes with large ovate-lanceolate bracts), 5-7-rayed (primary rays .5-2.5 cm. long), 3- or 4-times branched, bracteolate (the bractlets linear, up to 3.5 mm. long, deciduous) calyx tube about 1.2 mm. long, sparingly glandular-punctate or nearly glandless, the lobes triangular, .5-.7 mm. long, acute, strongly ciliate; corolla about 1.3 mm. in diameter at base, 2.8-3 mm. long, the lobes rounded, about 1.7 mm. wide; ovary terete; fruit broadly ovoid, 6-8 mm. long, 5-6 mm. in diameter, black.

COLOMBIA: El Cauca: Near La Topa and El Pedegral, Central Andes, east of Popayán, 1300-1600 m., *Lehmann 5161* (N, photo of type of *V. Urbani;* K). San José, west of Popayán, 2600 m., *Pennell & Killip 7383* (N,Y). Escaleretas, Río Paez basin, 2500-3000 m., *Pittier 1356* (N). Near Popayán, 1800 m., *Lehmann 831* (N), 3548 (N), 7941 (F).—ECUADOR: Mt. Pichincha, *Hartweg* (N, photo and fragment of type; Y, photo). Cuenca: Chagal, 2000-2500 m., *Lehmann 7940* (N, photo; K. Cited as *V. anabaptista* Graebn. in Bot. Jahrb. **37**: 435).

Perhaps more than a single species is represented by the material here cited, but we have not been able to find reliable characters upon which separate species can be based. Apparently the habit of the plants is quite variable. Lehmann's *5161*, the type of *V. Urbani*, is said to be a liana-shrub with elongate branches. *Viburnum pichinchense* is merely described as a shrub, 8 to 12 feet high, but the type specimen suggests a plant of rather lax habit. The plants of Norte de Santander, which we place in the following subspecies, were all compact shrubs with short branches.

The Pennell & Killip specimen from southwestern Colombia closely agrees with the type specimen from Mt. Pichincha. In other material from that region the pubescence is less dense on the under surface of the leaves, which are broader and more noticeably denticulate. Pittier's *1356* has large persistent bracts up to 1.5 cm. long. Graebner referred Lehmann's *7940* to *V. anabaptista*, a Costa Rican species. A specimen of this, courteously lent by the Director of the Royal Botanic Gardens, Kew, agrees closely with other material here placed in *V. pichinchense*.

2a. **Viburnum pichinchense toledense** subsp. nov. Compact shrub or small tree, 3-6 m. high, with short branches; leaves in two's and three's, ovate or oblong-ovate, 4-7 cm. long, 2.5-5 cm. wide, very densely grayish- or rufo-tomentose below, strongly impressed-nerved above; inflorescence twice-branched, few-flowered.

Type, *Killip & Smith 20589*, collected March 12, 1927, on eastern slope of Páramo del Hatico en route from Toledo to Pamplona, alt. 2800 m., Dept. Norte de Santander, Colombia, and deposited in the U. S. National Herbarium (no. 1,355,614). Duplicates at A, G, Y. Other specimens are: Norte de Santander: Divide between Río La Teja and Río Mesme, 2800 m., *Killip & Smith 19911* (A, G, N, Y). Toledo, 1800 m., *Killip & Smith 20107* (A, G, N, Y). Tapatá, 2300 m., *Killip & Smith 20184* (A, G, N, Y). Páramo del Hatíco, 2900 m., *Killip & Smith 20615* (A, G, N, Y).

This may be specifically distinct from *V. pichinchense* on the basis of its compact habit and smaller leaves, which are often in three's.

3. VIBURNUM GLABRATUM H. B. K. Nov. Gen. et Sp. **3**: 428. 1818. Tree; branchlets, rays of inflorescence, and petioles densely canescent-pulverulent; petioles 5-8 mm. long; leaves ovate-oblong, 8-13 cm. long, 4-5 cm. wide, obtusely acuminate at apex,

rounded at base, entire, glabrous, occasionally canescent-pulverulent on the nerves above; corymbs 5-10 cm. wide, bracteate (bracts ovate-oblong, about 1.5 cm. long, soon deciduous), 6- or 7-rayed, 2- or 3-times branched, bracteolate, the bractlets deciduous; calyx tube about 1 mm. long, essentially glabrous, the lobes .5-.6 mm. long, obtuse or acute, short-ciliate towards apex; corolla about 1 mm. in diameter at base, 1.7-2 mm. long, the lobes ovate, rounded, 2 mm. wide; fruit globose-ovoid, 5-7 mm. in diameter.

COLOMBIA: Cundinamarca: Fusagasugá, *André K444* (Y). Quetamé, 1400 m., *Pennell 1760* (N, Y). Huila: Neiva, 1500 m., *Rusby & Pennell 955* (N, Y). Tolima: Ibagué ?, 1000-1500 m., *André K445* (F, Y). Ibagué, *Hazen 9536* (N, Y).

By far the greater part of the Andean material of *Viburnum* has been referred to this species, apparently with little justification. The description of the indument of the type specimen as 'tenuiter canescenti-pulverulentes' applies only to a small part of the specimens examined in connection with this revision, and in Columbia true *V. glabratum* apparently has only a limited range. The original description states that the plant has two or three bracts, similar to the leaves but smaller. In Pennell's no. *1760* and André's *K445* these bracts are present, but in the other material here cited they are wanting, though quite possibly they may have been present at an earlier stage.

4. VIBURNUM TRIPHYLLUM Benth. Pl. Hartw. 189. 1845. Shrub or small tree; branchlets terete, hirsute with simple or usually stellate hairs or glabrescent; leaves often in three's (especially the upper ones), ovate or ovate-oblong, 4-8 cm. long, 2-5 cm. wide, rounded or acutish at apex and base, entire, thick-coriaceous, lustrous, glabrous or usually hirsute-tomentose in the axils of the nerves beneath, the nerves usually impressed above; peduncles stout, 3-6 cm. long; corymbs sometimes bracteate, 4-7 (rarely to 9) cm. wide, 6-8-rayed, 2- or 3-times branched, the rays rufo-hirtellous with simple or stellate hairs; calyx tube 1.6-1.8 mm. long, sparingly glandular-punctate, the lobes about 1 mm. long, subacute, ciliate; corolla about 1.5 mm. in diameter at base, 3.7-4 mm. long, the lobes oblong, rounded, about 2.1 mm. wide; fruit ovoid.

COLOMBIA: Cundinamarca: Zipaquirá, *Hartweg 1040* (Y, type collection, N, photo). Bogotá, 2900 m., *Pennell 2006* (Y); *Dawe 156* (N); *Ariste Joseph B105* (N); *Holton 443* (Y). Chiquin-

quirá, *Ariste Joseph B106* (N). La Calera, *Ariste Joseph A501* (N). Antioquia: Peñol, 2500 m., *Lehmann CCXV* (N). El Cauca: Paleterá to Calaguala, 3100 m., *Pennell 7102* (N, Y). Coconuco, 2500m., *Killip 6804* (N).—ECUADOR: Carchi: Ibarra, 3000 m., *Hitchcock 20940* (N, Y). Loja: Tablon de Oña, *Rose 23097* (N, Y). Azuay: Cuenca, *Jameson* (N).

This species is readily recognized by the very thick, coriaceous leaves, which frequently are in three's. The corymbs are more compact than in other close relatives. Much material usually referred to *V. glabratum* belongs to this species.

5. **Viburnum apiculatum** sp. nov. Shrub, up to 5 m. high, with large, profusely ramified branches; branchlets terete, essentially glabrous; petioles about 1.5 cm. long; leaves 'sea-green,' obovate, rarely oblanceolate, 5-12 cm. long, 4 to 5.5 cm. wide, cuspidate or apiculate at apex, subacute at base, subentire or sinuate-denticulate, glabrous above, stellate-tomentose on under side along midnerve, the nerves 5 or 6 to a side, parallel, nearly straight, anastomosing close to margin; peduncles stout, 5 to 7 cm. long, minutely stellate-tomentose towards apex; corymbs bracteate (bracts linear, about 1 cm. long), 10 cm. wide, 6-rayed, 2- or 3-times branched (ultimate branchlets very slender), finely stellate-tomentose, bracteolate, the bractlets linear-spatulate, about 7 mm. long, 1.5 mm. wide, acute; calyx tube 1.1-1.3 mm. long, densely glandular-punctate, the lobes ovate, about .9 mm. long, acute, not ciliate; corolla 'white, frequently washed over with pink,' 1.8 mm. in diameter at base, about 4 mm. long, the lobes oblong, rounded, 2.1 mm. wide.

Type, *Lehmann 5160,* collected at Coconuco, east of Popayán, Department El Cauca, Colombia, alt. 2200-2700 m., and deposited in the U. S. National Herbarium (no. 1,420,308). Duplicate F.

6. **Viburnum suratense** sp. nov. Tree 3-6 m. high, with a slender trunk, the branchlets terete, sparingly to densely rufo-stellate-tomentose; petioles 5-10 mm. long; leaves obovate or oblanceolate, 5-10 cm. long, 2-5 cm. wide, abruptly acuminate at apex with an obtuse triangular tip, subacute at base, entire or with a few minute teeth, glabrous or very sparingly stellate-pubescent above, glabrous or stellate-hirsutulous on the nerves beneath; peduncles stout, 4-10 cm. long; corymbs ebracteate, 6-10 cm. wide, 5-7-rayed, 2- or 3-times branched, densely or sparingly stellate-hirsutulous, bracteolate with minute deciduous linear bractlets; calyx tube 1.6-2 mm. long, glabrous, very sparingly glandular-punctate, the lobes triangular, slightly ciliate towards apex; corolla white, about 1.8 mm. in diameter at base, 3.8 mm. long, the lobes

ovate, rounded, 2.5 mm. wide; ovary slightly furrowed; fruit black.

Type, *Killip & Smith 16743*, collected Jan. 6, 1927, in the Río Suratá Valley, above Suratá, Dept. Santander, Colombia, alt. 2000-2300 m., and deposited in the herbarium of the New York Botanical Garden. Duplicates A, G, N. Other collections are: Santander: Mountains east of Las Vegas, 3200 m., *Killip & Smith 15864* (A, G, N, Y). Quebrada de País, north of La Baja, 3200 m., *Killip & Smith 18766* (N, Y). Dept. Cundinamarca: Bogotá, *Dawe 168* (N).

7. **Viburnum fragile** sp. nov. Small tree; branchlets slender, terete, rufo-stellate-hirsutulous, at length glabrous; petioles 3-5 mm. long; leaves ovate, 4-6 cm. long, 2-3 cm. wide, abruptly acuminate at apex, rounded or acutish at base, denticulate near apex (teeth minute, salient, each terminating a distinct vein), sparsely stellate-hirtellous above, distinctly so near the margins, which are slightly revolute and give the appearance of being ciliate, beneath stellate-tomentose on nerves, otherwise glabrous; peduncles slender, 3-4 cm. long; corymbs ebracteate, up to 4 cm. wide, rufo-hirsutulous with simple or stellate hairs, 5-rayed, 2- or 3-times branched, bracteolate, the bractlets linear-spatulate, about 2 mm. long; calyx tube 1.4-1.6 mm. long, glandular-punctate, the lobes ovate, about 1.1 mm. long, acute, sparsely ciliate; corolla white, 1.4-1.6 mm. in diameter at base, about 3.7 mm. long, the lobes oblong, 2.4-2.7 mm. wide.

Type, *Rusby & Pennell 757*, collected August 3-5, 1917, at Basillas, Dept. Huila, Colombia, alt. 2100-2200 m., and deposited in the herbarium of the New York Botanical Garden.

8. **Viburnum leptophyllum** sp. nov. Slender shrub or small tree 3-6 m. high, glabrous throughout or minutely and sparingly appressed-hirtellous along the ultimate branchlets, petioles, and rays of the inflorescence; petioles up to 1 cm. long; leaves ovate or oblong-ovate, 5-12 cm. long, 2-6 cm. wide, obtuse or obtusely acuminate at apex, acute or rounded at base, entire, herbaceous, lustrous on both surfaces, the nerves slightly impressed above; peduncles stout, 4-5 cm. long; corymbs ebracteate, 6-8 rayed, 2- or 3-times branched, bracteolate, the bractlets linear, about 3 mm. long; calyx tube about 1.5 mm. long, glabrous, very sparingly glandular-punctate, the lobes ovate, about 8 mm. long, acute or obtusish, short-ciliate; corolla about 2 mm. in diameter at base, 3-3.3 mm. long, the lobes oblong, subacute, about 2.1 mm. wide; ovary slightly furrowed; fruit globose or globose-ovoid, 7-8 mm. long, 5-6 mm. wide, dark blue or black.

Type, *Killip & Smith 17055*, collected Jan. 13, 1927, vicinity of California, Dept. Santander, Colombia, alt. 2300 m., and deposited in the U. S. National Herbarium (no. 1,352,712). Duplicates A, G, Y. Other collections are: Dept Santander: California, 2300 m., *Killip & Smith 16931* (A, G, N, Y), *17059* (G, Y), *17083* (A, G, N, Y). Charta, 2400 m., *Killip & Smith 19098* (A, G, N, Y), *19226* (A, G, N, Y), *19310* (A, G, Y). Suratá, 2200 m., *Killip & Smith 16628* (A, G, N). Las Vegas, 2800 m., *Killip & Smith 16083* (A, G, N, Y).

8a. **Viburnum leptophyllum venezuelense** f. nov. Leaves ovate or narrowly oblong, 3-7 cm. long, 1-3 cm. wide, thin-herbaceous, the nerves scarcely impressed; peduncles slender, 2-4 cm. long; calyx tube glandular-punctate with a few scattered short hairs; corolla 2.8-3.2 mm. long; ovary terete or slightly furrowed.

Type, *E. Pittier 94*, collected Oct. 25, 1921, in mountains near Galipán, Federal District, Venezuela, and deposited in the herbarium of the New York Botanical Garden. Duplicate N. Other collections are: VENEZUELA: Macaroa, 1500 m., *Jahn 474* (N, Y). Federal District: Galipán, 1700 m., *Eggers 13575* (N); *E. Pittier 91* (N). Caracas, *Kuntze 1667* (Y); Eggers *13229* (N); *Allart 83* (N, Y); *Pittier 7406* (N); *Curran & Haman 1125* (N). Coastal Range, *Pittier 8129* (N). Miranda: Los Teques, 1500 m., *Pittier 6486* (N). Mérida: Páramo Quirorá, 2600 m., *Jahn 884* (N). Páramo de Morro, 2800 m., *Jahn 1058* (N). Mérida, 1700 m., *Pittier 12857* (N, Y).—COLOMBIA: Santander: Mesa de los Santos, 1500 m., *Killip & Smith 15006* (A, G, N, Y), *15068* (A, G, N, Y), *15116* (A, G, N, Y).

This species appears to be confined to the mountains of northeastern Colombia and western Venezuela. In the Venezuelan material the leaves are smaller and thinner, and the rays of the inflorescence very slender. Gradations between this and typical *V. leptophyllum* are found in the Colombian specimens from the Mesa de los Santos.

9. **Viburnum floccosum** sp. nov. Tree or shrub, 2.5-5 m. high, with terete branches and branchlets, the branchlets and rays of inflorescence densely rufo-stellate-tomentose with matted hairs; petioles 5-8 mm. long; leaves oblong or ovate-oblong, 7-12 cm. long, 3-6 cm. wide, obtuse or obtusely acuminate at apex, rounded at base, coriaceous, sparingly stellate-pubescent on nerves and veins; peduncles very stout, up to 8 cm. long; corymbs

ebracteate, about 10 cm. wide, 7-10-rayed (rays nearly straight, ascending), 2- or 3-times branched, bracteolate, the bractlets about 1.5 mm. long, soon deciduous; calyx tube 1.3 mm. long, glandular-punctate, the lobes ovate, .7-.8 mm. long, acutish, ciliate (cilia up to .3 mm. long); corolla white, about 2 mm. in diameter at base, 4 mm. long, the lobes oblong, about 2.2 mm. wide.

Type, *Killip & Smith 18082,* collected Jan. 24, 1927, in oak forest, vicinity of La Baja, Dept. Santander, Colombia, alt. 3500 m., and deposited in the U. S. National Herbarium (no. 1,353,553). Duplicates A, G, Y. Other specimens are: Dept. Santander: California, 3000 m., *Killip & Smith 16916* (A, G, N, Y). Charta, 2000 m., *Killip & Smith 18869* (A, G, N, Y).

10. VIBURNUM DIVARICATUM Benth. Pl. Hartw. 132. 1844. Shrub, 2.5-4 m. high, with lax, densely stellate-pubescent branchlets, the upper internodes 5-8 cm. long; petioles 5-10 mm. long; leaves ovate-elliptic or oblong, 6-8 cm. long, 2-4 cm. wide, acuminate or subobtuse and short-cuspidate at apex, rounded or acutish at base, subentire, sparsely stellate-pubescent on both sides, the nerves 4 or 5 to a side, relatively distant; peduncles 6-8 cm. long, somewhat curved, densely stellate-pubescent; corymbs ebracteate, up to 10 cm. wide at anthesis (broader in fruit), 2- or 3-times branched, about 7-rayed, the rays slender, wide-spreading, the flowers not clustered, distinctly pediceled, with 2 minute sessile, setaceous bractlets at base; fruit oblong, 4-5 mm. long (immature).

Ecuador: Mount Paccha (N, photo of type).

This species, known to us only from a photograph of the type, is characterized by a lax, wide-spreading inflorescence, the flowers being quite distinct from each other, even at anthesis. In this respect it resembles *V. cornifolum (Killip 11648),* a species with distinctly oval leaves, which have conspicuous caudate-tips.

11. **Viburnum cornifolium** sp. nov. Shrub or small tree; branchlets terete, essentially glabrous, reddish brown; petioles 4-5 mm. long, minutely appressed-hirtellous; leaves ovate or oblong-ovate, 7-14 cm. long, 4-7 cm. wide, caudate-acuminate (tip sometimes to 2.5 cm. long), subacute at base, entire, glabrous above, or usually minutely stellate-hirtellous on the midnerve, essentially glabrous beneath, the nerves 5 or 6 to a side, arcuate-ascending; peduncles 5 to 10 cm. long, minutely stellate-tomentose; corymbs ebracteate, up to 12 cm. wide, 6- or 7-rayed, 3- or 4-times branched, ebracteolate, the rays finely hirtellous; calyx tube about 1.2 mm. long, glabrous, glandular-punctate, the lobes semicircular, 0.5 mm. long, finely ciliate; corolla 1.3 mm. in diameter at base, about 2.7 mm. long, the lobes ovate, 1.8 mm. wide.

Type, *Killip 11648*, collected Sept. 24-29, 1922, at Pavas, Dept. El Valle, Colombia, alt. 1700-2100 m., and deposited in the U. S. National Herbarium (no. 1,143,262). Duplicate Y. Other collections (also from Colombia) are: Dept. Antioquia: Valparaiso, vicinity of Medellín, *Toro 1377* (Y), with larger flowers, the corolla up to 3.5 mm. long, the lobes proportionately broader, 2.3 mm. wide. El Valle: Calima, *Killip 11206* (N, Y).

12. **Viburnum Lehmannii** sp. nov. Shrub or tree (?); branchlets terete, densely hirsutulous; petioles 5-8 mm. long; leaves oblong-lanceolate, 5-10 cm. long, 2-4 cm. wide, acuminate at apex, rounded at base, entire, glabrous or sparsely stellate-pubescent above, sparingly stellate-hirsutulous beneath, the nerves 4 or 5 to a side, arcuate-ascending; peduncles 2-6 cm. long; corymbs 3-5 cm. wide, rufo-hirsutulous with simple or stellate hairs, bracteate (bracts linear, about 7 mm. long, deciduous), 6- or 7-rayed, 3-times branched, bracteolate, the bractlets linear-spatulate, 2-3 mm. long; calyx tube about 1 mm. long, glandular-punctate, with a few scattered slender hairs, the lobes ovate, about .6 mm. long, acutish, sometimes slightly ciliate; corolla 1.3 mm. in diameter at base, about 2.5 mm. long, the lobes oblong, 1.6 mm. wide.

Type, *Lehmann BT671*, collected Feb., 1884, in highlands of Popayán, Dept. El Cauca, Colombia, alt. 1500-2000 m., and deposited in the herbarium of the New York Botanical Garden. Duplicate N. Another specimen is: El Cauca: Silvia, north of Popayán, *Lehmann 969* (Y).

13. **Viburnum Toronis** sp. nov. Tree or shrub; branchlets terete, essentially glabrous, lustrous; petioles 3-5 mm. long; leaves nearrowly oblong, 10-17 cm. long, 3.5-5.5 cm. wide, long-acuminate at apex (tip 1-1.5 cm. long), subacute at base, entire or subentire, glabrous above or the midnerve often minutely tomentellous, glabrous beneath; peduncles stout, 7 cm. long; corymbs ebracteate, wide-spreading, up to 13 cm. wide, 6-rayed, bracteolate, the bractlets ovate-lanceolate, up to 3 mm. long; calyx 4- or 5- times branched, the branches finely stellate-to mentulose, tube .8 mm. long, sparsely glandular-punctate, the lobes ovate, about .8 mm. long, acutish, faintly ciliate; corolla 1-1.3 mm. in diameter at base, about 2 mm. long, the lobes oblong, 1.6 mm. wide.

Type, *Toro 424*, collected Aug. 20, 1927, at Medellín, Dept. Antioquia, Colombia, and deposited in the herbarium of the New York Botanical Garden. Duplicate N.

INDEX TO AMERICAN BOTANICAL LITERATURE

1926-1929

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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